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A THEORETICAL AND EXPERIMENTAL  
ANALYSIS OF ADAPTATION TO ASYMMETRICAL  
AND DISTORTED VISUAL STIMULATION

BY

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THESIS SUBMITTED FOR THE  
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A Theoretical and Experimental  
Analysis of Adaptation to Asymmetrical  
and Distorted Visual Stimulation

General Introduction

Throughout the nineteenth century there was philosophical and psychological interest in the problem of the optically inverted retinal image. Out of this speculative interest grew Stratton's classic experimental studies with inverting spectacles. This work will be reviewed in detail in chapter 1, suffice it to point out here that interest in this problem declined until the 1930's when work of two men revived interest in it. In 1933, J. J. Gibson was studying the effects of wearing distorting prisms and accidentally discovered that the inspection of curved lines caused subsequently seen, straight lines to appear curved the other way. An analogous effect for tilt was also reported. This class of phenomena came to be called adaptation or normalization. The other man to revive interest in the effects of prismatic visual distortions was T. Erisman, working in Innsbruck. He repeated, more systematically, the experiments of Stratton, and later, his assistant Ivo Kohler, extended the work to include many types of visual distortion.

There thus appear to be two classes of inducing condition; one involving visual asymmetry in relation to a norm or neutral stimulus value, the other involving distortions of the visual input relative to the motor system and the other sense modalities. At the same time, there appear to be two types of effect, one involving purely visual judgments, such as curvature of the visual vertical, the other involving visual-motor

co-ordination.

It was generally assumed for some time that the judgmental effects were caused by asymmetrical visual stimulation, and that the visual-motor effects were caused by prismatic displacements or rotations of the visual input. Evidence now shows that this is not so; both judgmental and visual-motor effects may be produced by asymmetrical stimulation as well as by a disturbed visual input in the absence of visual asymmetry. It is important to consider normalization when dealing with the consequences of wearing optical distorting devices because such devices usually introduce some asymmetry which may contaminate the results unless care is taken. Most, if not all <sup>of</sup> the reported experiments on visual distortion are so contaminated.

The aims of this thesis are: 1) to demonstrate by a critical evaluation of the literature and experimental procedures that normalization is a real phenomenon distinct from figural after-effects and the effects of eye movements, 2) to demonstrate a normalization effect in the judgment of relative depth, and 3) to analyse the behavioural consequences of wearing distorting optical devices - both those due to visual asymmetry and those due to sensory motor and intersensory discordance.

The work was not planned as a whole but emerged over the years and was dictated by chance discovery, planned hypothesis, an attempt to make relevant distinctions and comparisons, and common curiosity.

Much of the work was supported by grants from the D.S.I.R. and, for much of it, the assistance was had of Mr. W. B. Templeton and later of Mr. B. Craske. The theoretical analysis was always my own, although discussion with the assistants was of great help. The various pieces of apparatus were always basically my design and usually made by me, with the help of Mr.

Craske and Mr. J. Evans, the technician. Both Mr. Templeton and Mr. Craske helped with the administration of the experiments and Mr. Templeton with the analysis of the data, especially those reported in chapter 3. Most of the work has been published in several publications. My thanks are due to Professor F. V. Smith for his advice.

SECTION I

Adaptation to Asymmetrical Visual Stimulation

CHAPTER 1TILT ADAPTATION

Basic Facts. In 1933 J. J. Gibson accidentally discovered a phenomenon during an experiment on the effects of wearing distorting prisms. Prisms not only cause an apparent displacement of the visible world but also introduce an apparent curvature. Gibson found that the extent of the apparent curvature diminished as the subject continued to wear the prisms. When the prisms were removed, straight lines appeared to be curved in the opposite direction to the direction of apparent curvature induced by the prisms. This after-effect was produced whether or not the subject manipulated the environment and whether or not he moved his eyes, and is therefore not due to conflict between visual and kinaesthetic experiences. Even without prisms, curvature apparently diminished during inspection of a curved line, and a straight line seen subsequently in the same location appeared curved the other way, Verhoeff had reported this last effect in 1925. Gibson also noted that a straight line seen against a background of curved lines appeared to be curved the other way. This simultaneous effect had been known for some time, as Gibson realized.

Gibson conducted several experiments which demonstrated that the after-effect of seen curvature is restricted to the retinal locality stimulated by the inspection figure. For example, if a curved line was inspected for several minutes and then several straight lines were exposed together, only that straight test line which coincided with the position of the previous inspection line showed the apparent curvature. There was some evidence of a slight spread of the after effect from one locality to another but Gibson concluded that most of the effect is limited to the position of the inspection line.

Gibson presented the inspection figure to one eye and the test figure to the other and found that the after-effect transferred to almost its full extent. This interocular transfer of the effect was said to demonstrate its origin beyond the level of the chiasma, a conclusion we shall presently question.

An analogous adaptation effect was later found for tilted lines (Gibson and Radner 1937). Inspection lines which were off-vertical caused vertical lines seen subsequently to appear tilted in the opposite direction. Vernon (1934) had reported a similar effect and she interpreted Gibson's curvature adaptation effect as a normalization to the vertical of the parts of the curved line. Such an explanation would account only for curvature after-effects produced by vertically oriented curved lines. Gibson showed that the curvature after-effect is not dependent on the orientation of the inspection line, and thus disproved Vernon's suggestion.

The tilt after-effect was considered by Gibson and Radner to be analogous to the curvature after-effect. Both phenomena were explained in terms of adaptation processes in oppositional scales. Examples of oppositional scales are 'up and down' in relation to the stationary state and 'tilt right and tilt left' in relation to the vertical. In each case there is a neutral point in the scale. So-called intensive scales, on the other hand, do not pass through a neutral value; examples are weight, distance, and loudness.

The neutral point in an oppositional scale is the norm, it is the point from which the intensities of the scale values increase in either direction. It is the most frequent value of the scale to be experienced. In many cases it is the point in the scale which is discriminated most acutely.



All oppositional scales probably exhibit normalization, that is, stimuli which are off the norm come to be reported as being more like the norm as they continue to be inspected. Inspection of an off-norm stimulus produces an alteration over the whole scale in the correspondence between the physical values of the scale and the reported magnitudes, although this shift in correspondence may be maximal in the region of the inspected value. Such a shift persists for some time and manifests itself as an after-effect when subsequent judgments are made. Gibson wrote, "If a sensory process which has an opposite is made to persist by a constant application of its appropriate stimulus-conditions the quality will diminish in the direction of becoming neutral, and therewith the quality evoked by any stimulus for the dimension in question will be shifted temporarily towards the opposite or complementary quality" (page 223).

I am only concerned here with visual spatial dimensions. There are several spatial dimensions which are oppositional.

- (a) Tilt or rotation of a line (or other figure) from the vertical or horizontal in the frontal or sagittal plane; rotation of a line in the horizontal plane from the pointing-straight-ahead position or from the frontal-parallel position (making three dimensions with two norms in each).
- (b) Translation of a line (or other figure) from the median plane to left or right. Translation of a line from the horizontal plane up or down. (Making two dimensions with one norm each).
- (c) Departure from straightness by curvature or bending in the frontal plane or in depth.

I shall be concerned largely with tilt in the frontal plane. When a tilted line gradually comes to appear less tilted, it is said to normalize to the vertical. The after-effect of inspecting an off-vertical line on

a subsequently seen vertical line is called the tilt after-effect. It is not easy to measure normalization directly and it has often been assumed that the extent of the tilt after-effect is a measure of the normalization which the inspection figure has undergone. This would be true only if the shift of the subjective scale were homogeneous throughout the stimulus range, and if there were no other mechanisms which could account for, or influence the tilt after-effect. It will be shown later that neither of these assumptions is justified.

Gibson (1937a and b) and Gibson and Radner (1937) found the tilt after-effect to have the following properties. Like the curvature after-effect, it is limited to the location of the inspection figure, although it does transfer from one eye to the other. The amount of after-effect rapidly rises as the duration of the inspection period is increased, levelling off at  $1.5^{\circ}$  after between 45 and 90 sec inspection of a  $5^{\circ}$  tilted line. As the tilt of the inspection line is increased, the after-effect increases to a maximum for an inspection tilt of between  $5^{\circ}$  and  $20^{\circ}$ . For greater tilts, the after-effect falls off, reaching zero when the inspection line is about  $45^{\circ}$ . With an inspection line of more than  $45^{\circ}$ , the whole scale shifts towards the horizontal. A vertical test line is also apparently shifted, but now towards the position of the inspection line. In a similar way horizontal test lines are affected by inspection lines near the vertical. These reversed effects of inspection lines on test lines in neighbouring quadrants are known as indirect effects; they are not as marked as the direct effects. Table 1 shows the results which Gibson and Radner (1937) obtained for the effect on the vertical and horizontal of inspection lines tilted  $5^{\circ}$  from the vertical or the horizontal and inspected for 45 sec.

Inspection line 5° from Vertical		Inspection line 5° from Horizontal	
Direct	Indirect	Direct	Indirect
1.09°	0.54°	1.42°	0.75°

TABLE 1 Showing the amount of the direct and indirect tilt after-effect obtained for a 5° tilted line inspected for 45 sec (Gibson and Radner 1937).

These are basic facts about tilt adaptation which were discovered by Gibson and Radner. It has been found that when subjects are asked to set a line to the vertical, they tend to set it to the side to which it was initially tilted (Werner and Werner, 1952). The same effect has been reported when the body is set to the vertical. These effects are easily explained in terms of tilt adaptation.

McFarland (1962) has demonstrated that the tilt after-effect is accompanied by an apparent rotation of the body axis in the opposite direction. He suggested that a reflex tendency to set the body axis parallel with the tilted line contributes to the two perceptual changes.

Since Gibson and Radner's report, some workers have tried to demonstrate that the tilt after-effect can be explained in terms of other mechanisms, while others have tried to demonstrate that it is a distinct process. The following mechanisms could account for the tilt after-effect:

- 1) The after-effects of Gibsonian normalization to the vertical;
- 2) Adaptation to rotated visual frames in the manner of Wertheimer's tilted-mirror effect;
- 3) Simultaneous-contrast effects of direction such as are seen in the Hering illusion;
- 4) Figural after-effects.

Gibson's tilt adaptation will be compared and contrasted with each of the other processes in turn.

Tilt Adaptation and Shifts of the Visual Frame. Gibson realized that tilt adaptation resembles Wertheimer's reported experience that the reflection of a room seen through a  $45^{\circ}$  tilted mirror appears to straighten after some

time. Witkin's visual frame effects are akin to the Wertheimer effect. Gibson, Held, Morant, and others have given reasons why these two phenomena should not be considered the same. I shall refer to one as Gibson's adaptation and the other as a visual frame shift. The suggested differences between them are listed below.

- (a) The Magnitude of Tilt Adaptation and Frame Shifts. Gibson's adaptation is never more than about  $3^{\circ}$ . Frame shifts have been found by Wertheimer (1912), Witkin (1949), and Bellar and Morant (1963) to be complete for angles of tilt up to about  $25^{\circ}$ .
- (b) Spatial Transfer of Tilt Adaptation and Frame Shifts. Gibson stated that tilt adaptation is largely localized to the site of the inspection figure. On the other hand, it is generally stated that frame shifts transfer to all parts of the visual field. Both these statements may be challenged. Morant and Mikaelian (1960) questioned Gibson's reasons for believing that adaptation does not transfer. One of Gibson's experiments involved the inspection of three lines side by side, two vertical lines and a middle one which was tilted. Of three vertical test lines, only the middle line, corresponding in position to the tilted inspection line, appeared tilted. Morant and Mikaelian pointed out that this experiment demonstrated only that different inspection lines could produce differential effects in different parts of the field, and did not test whether the after-effect is restricted to parts of the field which correspond to the position of inspection lines. Gibson showed that no after-effect of a tilted line can be seen in a test field consisting of an ordinary room. He suggested that

this is evidence that the effect does not transfer to all parts of the visual field. However, Morant and Mikaelian remarked that it demonstrates only that the tilt adaptation effect does not manifest itself when a strong vertical-horizontal frame of reference is present. They reported their own experiment, in which a tilted inspection line and a vertical test line were either exposed in the same location or in different locations,  $7^{\circ}$  of visual angle apart. An after-effect of  $1.52^{\circ}$  was obtained when inspection and test lines coincided and of  $1.09^{\circ}$  when they were separated. There was thus considerable transfer of the after-effect at least over  $7^{\circ}$  of the visual field. This is not a large distance, and the experiment should be repeated for different distances.

Morant and Mikaelian's criticisms of Gibson's evidence against transfer do not apply to Gibson's 1933 experiments, which Morant and Mikaelian did not mention. These experiments were on curvature adaptation rather than tilt adaptation but otherwise involved the same procedure as the experiment by Morant and Mikaelian. Gibson used separations of  $5.7^{\circ}$  of visual angle between his test and inspection figures and obtained transfer effects about one quarter as large as the effects with no separation between the figures. Thus Gibson did not deny that transfer of adaptation could take place; he insisted only that most of the effect is localized. More experiments are needed before anyone can say just how localized adaptation effects are.

I can find no experimental evidence to support the belief that

visual-frame shifts transfer to all parts of the retina. If prism distortion were limited to half the retina while the other half was blanked out, it is not known whether adaptation would transfer to the blanked-out region of the retina.

The distinction between Gibson's adaptation and frame shifts on the basis of transfer cannot therefore be accepted on these grounds as yet.

(c) Passive and Active Inspection in Tilt Adaptation and Visual Frame Shifts

Gibson found that tilt adaptation occurs whether or not the subject manipulates the inspection figure. It has been claimed that frame shifts depend on the active behaviour of the subject during the inspection period. Mikaelian and Held (1964) found a tilt adaptation effect of a few degrees after wearing prisms which rotated the optical array. This effect occurred when the subjects were passively wheeled about in a hallway. This passively produced after-effect was thought to be a Gibson adaptation effect. When the inspection field consisted of luminous spheres providing no cue to the distortion introduced by the prisms, then passive movement of the subject did not produce any tilt after-effect.

When the subjects moved about actively during the inspection period, both inspection fields produced tilt after-effects. The normal inspection field produced after-effects nearly as large as the  $20^{\circ}$  tilt introduced by the prisms.



Mikaelian and Held also found that passive inspection of a prismatically tilted field produced a Gibsonian tilt after-effect but did not produce any distortion in the apparent position of single points of light in the egocentric median plane. Active inspection on the other hand not only produced larger after-effects of tilt but also apparent displacements of points of light from the median plane. However, the reported absence of a displacement of dots in the passive condition may only have arisen because of the difficulty of measuring small apparent displacements of dots from the median plane.

Hochberg (1963) objected that the after-effects consequent upon active movement which Mikaelian and Held described were not true visual after-effects, in that they did not involve an intra-visual-field distortion. However, while Hochberg's paper was in press, Rekosh and Held (1963) and Held and Rekosh (1963) had produced evidence that active movement may induce curvature after-effects, which are certainly intra-visual (Held, 1963b). The results of the Mikaelian and Held experiments suggest that active movement is necessary for adaptation to rotations of the optical array through large angles. The special case of prismatic inversion of the optical array in which there is no displacement of the main visual lines relative to the egocentric axes, will be discussed in chapter 6.

Wertheimer, on the other hand, in the early experiment with a tilting mirror, did not report that active movement was necessary for the large apparent shifts of the field of view which he observed. Koffka and Witkin also reported almost full adaptations to large rotations of the field of view, and yet did not mention the necessity for active



movement.

Morant and Beller (in press) found that active movement doubled the effect of prismatic rotation obtained with a seated subject, provided the inspected field consisted of objects: active movement did not significantly change the after-effect when the field consisted of a series of parallel straight lines. With the object fields, active movement for 15 minutes produced a displacement in the apparent verticality of lines of almost  $4^{\circ}$  for a  $15^{\circ}$  tilt and almost  $8^{\circ}$  for a  $75^{\circ}$  tilt.

- (d) Tilt Adaptation and Frame Shifts for  $45^{\circ}$  of Tilt. The Gibson adaptation effect should be absent for inspection lines tilted at  $45^{\circ}$ . At this angle the opposed adaptation effects induced by the vertical and horizontal norms should cancel out. Gibson and Radner (1937) and Culbert (1954) found that this is the case, although Köhler and Wallach (1944) failed to substantiate this result. There is no reason why frame shifts should not occur for fields tilted at  $45^{\circ}$ . In fact Wertheimer obtained his effect with a field tilted at  $45^{\circ}$ .

Morant and Beller (in press) demonstrated that  $45^{\circ}$  tilts of a field consisting of objects affected the apparent verticality of a line whereas the same tilt of a field of parallel straight lines did not. Similarly the two fields when tilted to  $15^{\circ}$  produced congruent effects on the apparent verticality of a line whereas when tilted to  $75^{\circ}$  they had opposed effects: a field of lines adapts to the nearest main axis, whereas a field of normally upright objects always adapts to the vertical.

All this suggests that there are several factors which determine

the extent of adaptation to a tilted visual frame.

- (i) Active movement is necessary where the visual field itself gives no clue to the distortion, but even where it does, active movement will increase the effect provided that,
- (ii) the field of view contains familiar objects, and particularly when
- (iii) both the inspection and the test fields contain familiar objects.

These suggestions are not all proved by the foregoing evidence: further experimental work is necessary.

Tilt Adaptation and Simultaneous Tilt Contrast. Gibson was emphatic in his belief that the tilt after-effect is not the same process as simultaneous tilt contrast. A tilt-contrast effect is shown in figure 1. These effects were first described by Hoffman and Bielschowsky (1909) and later by Krantz (1930) and Kleint (1936). Gibson wrote, "Although the simultaneous contrast phenomenon bears an intriguing resemblance to the after-effect phenomenon, it is far from being the same thing and requires some hypothesis of its own" (page (568)). All the experimental evidence which Gibson reported showed that the simultaneous and successive effects behave alike. The operational basis for making a distinction is therefore not clear in Gibson's account. The successive effect take time to develop, whereas the simultaneous effect does not. But this does not provide a good basis for distinguishing between them, for if the after-effect is due to an after-image persisting from the inspection line, one would expect the successive effect to increase in strength as the after-image is strengthened by a longer exposure of the <sup>inspection figure.</sup> <sub>h</sub>

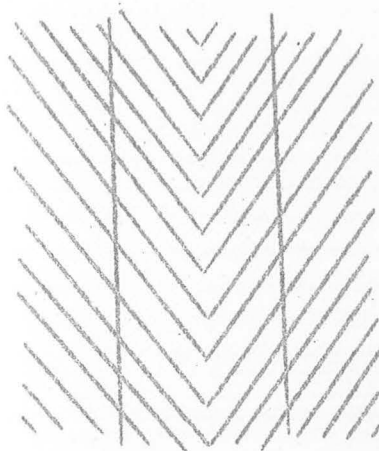


Fig. 1 A simultaneous tilt contrast effect.

One would also expect that the simultaneous effect should always be greater than the successive effect. Interocular transfer of the successive effect is no evidence that it is not dependent on after-images, for after-images persist when an eye is closed and may still affect the appearance of stimuli seen with the other eye.

Tilt Adaptation and Figural After-Effects. Köhler and Wallach (1944)

considered that Gibson's adaptation effects were a special case of a broader class of effects based on a mechanism which they called "satiation". According to satiation theory, Gibson's tilt after-effect is due to "electrotonic" spread of the striate cortex processes produced by the inspection line, which shift the site of the subsequent test line processes and hence produce an apparent repulsion of the test line away from the location of the inspection line. The magnitude of the repulsion depends on the distance between the locations of inspection and test lines; this means that the size of the tilt after-effect should depend on the angular separation of the two lines rather than, as Gibson thought, their relationship to the main visual axes.

There are several operational distinctions between Gibson's tilt after-effect and Köhler's figural after-effect. These are listed below.

(a) Normalization. Köhler's theory cannot account for normalization

itself, that is, the progressive decrease in the apparent tilt of an off-vertical line. A figural after-effect cannot have any effect on the apparent position of the inspection figure itself. Normalization of a tilted line is a commonly reported effect (for example, Gibson and Radner, 1937; Morant and Mistovich, 1960). I have already commented on the difficulty

of measuring normalization directly. There seem to be three procedures by which this can be done.

The most obvious method is to ask the subject to make absolute estimates of the tilt of a line on first sight, and again after a period of inspection. Templeton and Howard (to be published) conducted an experiment of this type, and found a significant adaptation of a  $5^{\circ}$  line to the vertical. Magnitude estimations of a series of lines, including one at  $5^{\circ}$ , were separated by periods of inspection of the  $5^{\circ}$  line.

The second procedure for measuring normalization is one first used by Prentice and Beardslee (1950). A 3 in. inspection line, tilted  $10^{\circ}$ , was exposed on one side of the fixation point. A 3 in. test line was then exposed at an equal distance on the other side of the fixation point. The subject had to report whether the test line was tilted more or less than the inspection line had been. Conditions were used in which the inspection line was surrounded (a) by an upright square with a 4 in. side, (b) by a square with a 8 in. side, (c) by an aperture in which the sides were parallel with the inspection line and (d) by a plain dark field. Neither the variations in the frame nor its absence had much effect on the normalization indicated by the method, which was about  $2^{\circ}$ . On Köhler's theory the inspection line should have tended to line up with the sides of the frame. But the fact that the different shapes and sizes of frame had no effect is evidence that this was not occurring.

These experiments were criticised by Heinemann and Marill (1954). They suggested that there were possibilities for figural after-effects even in the condition where the sides of the frame were parallel with the inspection line. This is because the frame had acute angles in two corners and obtuse angles in the other corners. Satiation is supposed to be denser

in acute angles. They repeated the experiments with modifications. In one condition, the inspection line was vertical but the frame (not just the sides) were tilted  $10^{\circ}$ . In another condition the inspection line and the whole frame were tilted  $10^{\circ}$ . In the first condition, the vertical line appeared to align with the edges of the frame. In the other condition, there was no significant tendency for the line to appear to turn towards the vertical, when the alignment effect was excluded. Thus the only effect found was one predictable from Kohler's theory.

Held (1963) adopted a similar procedure for measuring normalization. The inspection figure was a  $10^{\circ}$  tilted line. The test figure consisted of two  $10^{\circ}$  tilted lines, A and B: one of which (A) coincided with the inspection line. The subject fixated mid-way between the centres of the two lines and was first asked to set the comparison line parallel to the inspection line; this served as a control setting of parallelity. The inspection line alone was then exposed for 60 sec. after which the subject had to report which way line B had to be turned to be parallel with line A. Most of the reports were consistent with the presence of local tilt normalization to the vertical. There is a point of criticism to be made about this experiment. The geometric arrangement of the two lines was either as shown in figure 2a or as shown in figure 2b. The lines themselves were tilted clockwise and anti-clockwise from both the vertical and the horizontal, but this does not affect my argument. In figure 2a, the top end of the line B is nearer to line A than is the bottom end of line B. B should therefore appear tilted towards the vertical as compared with line A. This is in conflict with the prediction from Gibson's normalization. If the two opposed effects are of equal strength then

half the subjects would give judgments in favour of Gibson's hypothesis and half in favour of Köhler's. In the arrangement shown in figure 2b the bottom of line B is nearer the inspection line A than is the top of line B. Line B will therefore appear tilted further from the vertical than line A. This effect is in the same direction as the Gibson effect, and therefore all subjects should report in favour of Gibson's hypothesis. In total therefore about three quarters of the responses should favour Gibson's hypothesis and one quarter Köhler's. These are roughly <sup>the</sup> proportions of responses which Held reported. The geometrical arrangement which would have overcome this intrusion of a Köhler effect is shown in figure 2c. This pattern has a symmetrical relation between the two lines. X

Morant (private communication) could not reproduce Held's effect and attributes it to the fact that Held had his subjects set the comparison line parallel to the inspection line prior to the inspection period. It was always the inspection line which was adjusted, and Morant claims that this would lead to an 'error of the standard' which would provide a distorted control measure from which to measure the main effect.

Held's procedure has in any case a basic weakness, which he recognized: it measures only that part of normalization which does not transfer to the second test line. Held does not state the angular separation between his two lines, but if we assume that it was similar to the separation between the lines in Morant and Mikaelian's study, viz  $7^{\circ}$  (see page 10), then at least two thirds of the normalization effect transfers according to the results of that study. The procedure would

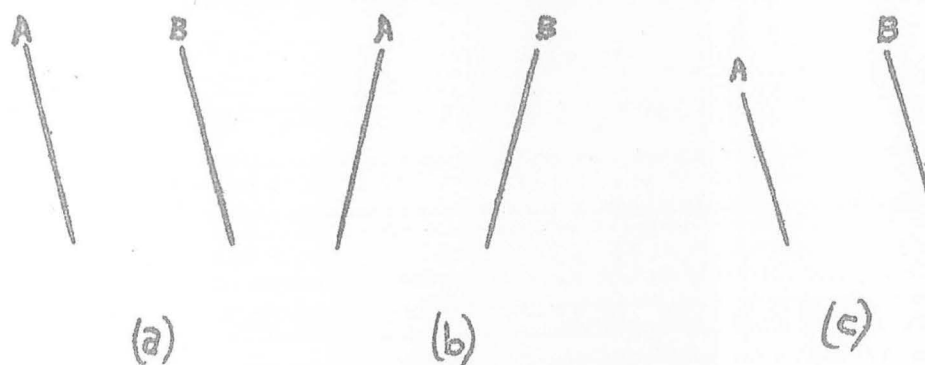


FIG. 2 . Arrangement of lines used in the experiment by Held (1963) to demonstrate tilt adaptation.



therefore record only a fraction of the normalization.

The third procedure for measuring normalization directly is one proposed by Templeton. The patterns used are shown in figure 3.

The inspection figure consists of two lines tilted symmetrically about the vertical. The test figure consists of the same lines as the inspection figure, with an extension of the two lines to form a symmetrical cross. If the two inspection lines normalize, the angle between them should appear to shrink. Thus, after inspection, the top angle in the test cross would appear to be smaller than the bottom angle, as compared with its apparent relative size before inspection. On the other hand, if a figural after-effect occurs, the top angle should appear relatively larger after inspection, than the bottom angle. A constant stimulus method was used to measure the actual effect. The net effect for all subjects was not quite significantly in favour of a Gibson effect. The situation is not simple. The simultaneous normalization of two lines in opposite directions suggests a complex deformation of the scale of inclination, with no actual shift of the norm itself - a phenomenon which would be easily integrated into Gibson's theory. Presumably, complex transfer effects would also operate.

In an experiment by Prentice and Beardslee (1950) the subjects tilted their heads so that the tilted inspection line fell on the normally vertical meridian of the eye; this was ensured by having them align the inspection figure with the after-image of a vertical line induced when the head was erect. The inspection figure, when compared with an objectively parallel line had clearly normalized to the



a. Inspection figure



b. Test figure

Fig. 3 . The arrangement used by Templeton to measure tilt normalization.

gravitational vertical. Prentice and Beardslee concluded that normalization is to a "psychological" rather than a retinal axis and hence even the postulation of permanent ~~sati~~ation gradients from top to bottom of the cortical projection of the retina would not enable Köhler's theory to encompass normalization.

(b) The Symmetry of the Figural After-Effect. Köhler and Wallach (1944) supported their argument that the Gibson effect was a case of figural after-effects by the following experiment. They measured the tilt after-effect produced on a vertical line by inspection of a  $10^{\circ}$  tilted line and compared this with the after-effect produced on a  $10^{\circ}$  tilted line by inspection of a vertical line. The two after-effects were similar, which fits the figural after-effect hypothesis but not Gibson's hypothesis, which predicts no after-effect of a vertical inspection line.

Templeton, Howard, and Easting (in press) repeated this experiment. The after-effect was measured by setting a second test line parallel with the test line which coincided with the previous inspection line.

There was a significant after-effect from vertical line to tilted line, but it was significantly smaller than the after-effect produced by the tilted line on the vertical line. This result suggests that both Gibson and Köhler type processes are operating.

(c) Relative Shifts of Different Parts of the Subjective Scale of Tilt.

A related study was conducted by Templeton and Howard (to be published). A line tilted  $5^{\circ}$  was inspected for one minute and then a test line was briefly exposed at one of ten angles between  $9^{\circ}$  clockwise and  $9^{\circ}$  anti-clockwise of the vertical. The subject had to estimate the inclination of the test line using whatever numerical categories he wished. The test lines were exposed, one at a time, interspersed with five second

'topping-up' exposures of the inspection line. In the control condition, the inspection line was replaced by an empty field. It was thus possible to assess the effect of an inspection line simultaneously on several different test lines. The predicted scale shift of Köhler's hypothesis is depicted in figure 4a and that predicted on Gibson's hypothesis in figure 4b. The results again suggest that both mechanisms are operating.

All displacements, including those of lines more tilted than the inspection figure, were in the direction predicted on Gibson's model, but the displacements fell to zero for the most distant lines i.e. those tilted more than  $5^{\circ}$  in the opposite direction to the inspection figure.

(d) The Indirect Effect. Gibson and Radner (1937) reported the indirect effect which I have already described. Briefly it is that exposure to a tilt off one axis produces an after-effect on the other axis. Köhler's theory cannot account for the indirect effect, but Köhler and Wallach (1944) and Prentice and Beardslee (1950) failed to confirm it experimentally. Morant and Mistovich (1960) reported findings which are in essential agreement with Gibson and Radner's results. The indirect effect was found to be approximately half the direct effect. Gibson had put this difference down to "play" between the axes. The greater distance apart of the test and inspection lines in the indirect condition as compared with the direct condition could explain this "play". Morant and Mistovich, on the other hand, interpreted the difference between the two effects as due to the summation of Gibson's tilt after-effect and Köhler's figural after-effect. Whichever view one takes, the evidence suggests that there

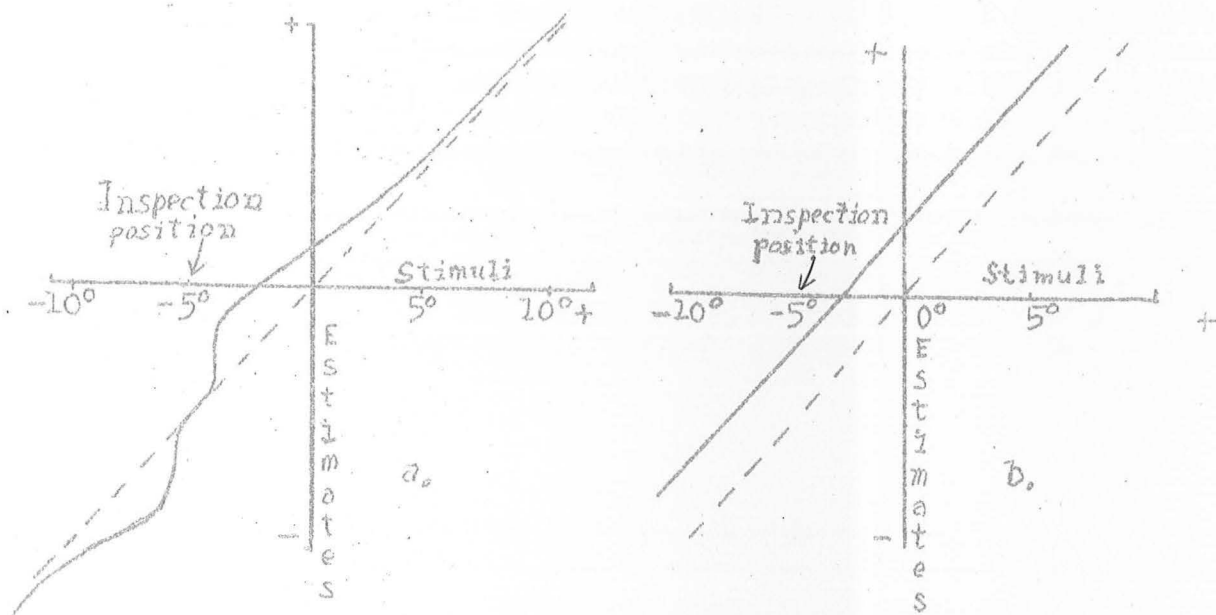


FIG. 4. The predicted scale shifts in absolute judgments of inclination after inspection of a line tilted to  $-5^\circ$  according to a) Köhler and b) Gibson.

is a Gibson effect.

Morant and Harris (1965) made prediction about the after-effects on a vertical test line produced by inspection lines at various angles between vertical and horizontal. The predictions were made assuming only a Gibson-type process on the one hand, and only a Köhler-type process on the other. Figures 5a and 5b show the shapes of the two predicted functions. Figure 5c shows the probable function assuming that both processes are operating and figure 5d shows the empirical function which they in fact found. The results are a good fit to the summated function in figure 5c. Contrary to the satiation hypothesis there is a cross-over point at which the effect is zero, but it occurs at about  $60^{\circ}$ , not at  $45^{\circ}$  as a purely Gibsonian hypothesis would predict.

This argument depends on the assumption that the vertical and horizontal norms are of equal strength. If the vertical norm is stronger than the horizontal norm then one would expect the null-point to be displaced towards the horizontal, and satiation would not have to be invoked in order to explain the results. Gibson reported that the horizontal norm was only slightly stronger than the vertical norm; Morant and Mistovich (1960a) that they are equally strong. Thus the assumption which Morant and Harris make seems justified. However, their interpretation also depends to some extent on the assumption that the Gibson effect transfers fully over all angular positions. If there were partial transfer only, this could account for the indirect effect being less than the direct effect. In so far as the crossover point is significantly different from  $45^{\circ}$ , their experiment supplies further evidence that there

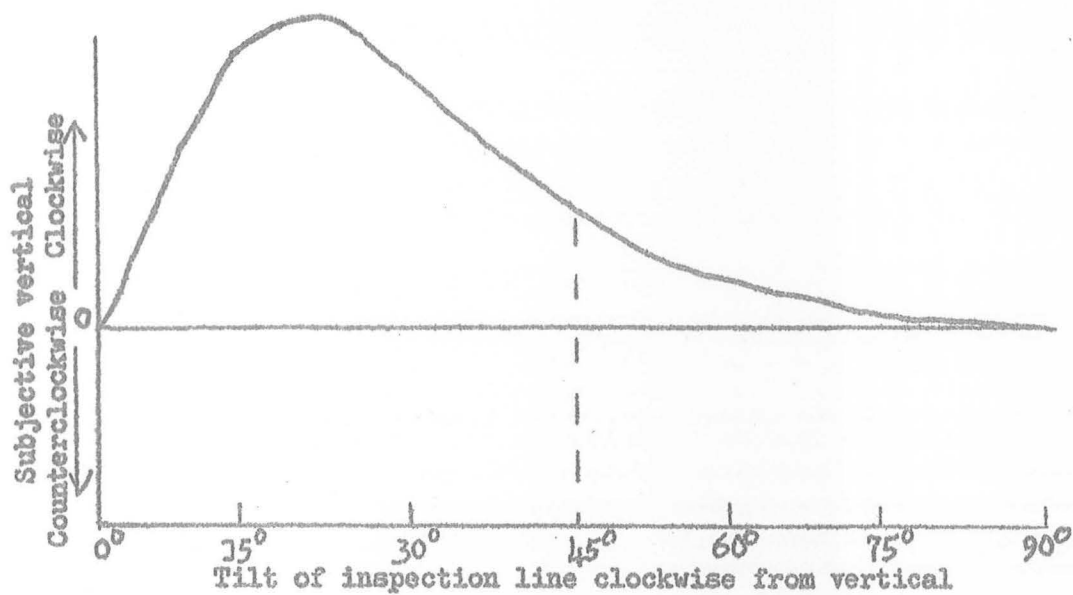


FIG.5a Hypothesized effects of "satiation" Process.

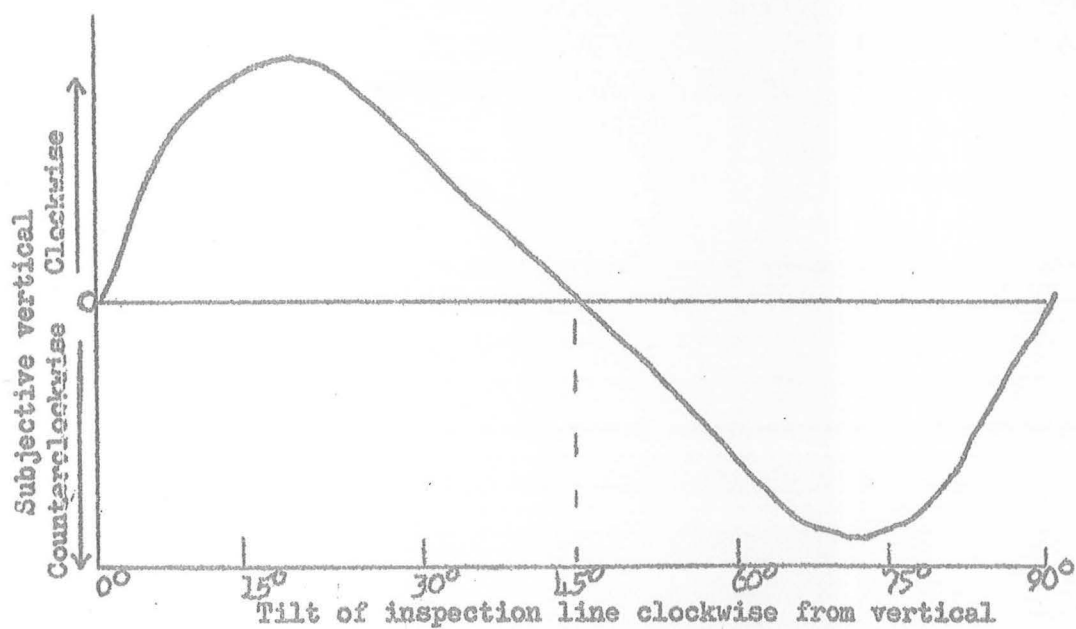


FIG.5b Hypothesized effects of "adaptation" process.

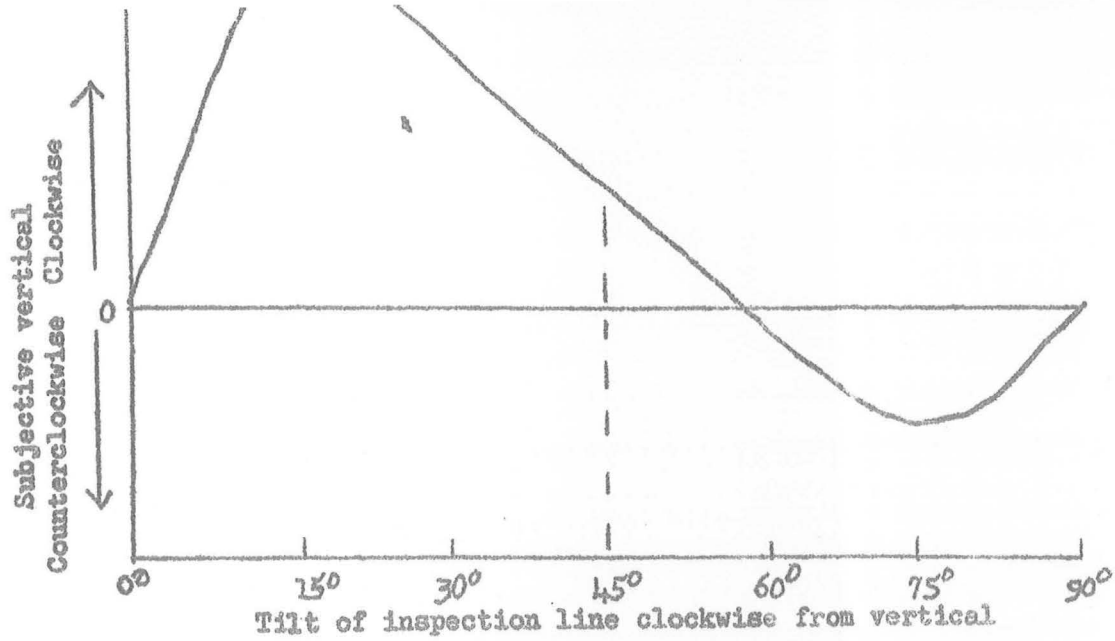


FIG. 5c Algebraic summation of "satiation" and "adaptation" effects.



FIG. 5d Measured amount of tilt after-effect for increasing amounts of tilt of the inspection line. (Morant and Harris, in press).



are both Gibson and K hler processes.

This view is supported by results reported by Fox (1951). In this study the inspection figure consisted of two squares; the bottom edge of one square and the top edge of the other were in a horizontal line. Fixation was between them. Two test dots coincident with the horizontal edges appeared displaced away from the centres of the squares. Fox considered that figural after-effects could not account for this effect especially when it was found that it was only present when the two squares were in this particular orientation to one another.

(e) Differential Transfer of Tilt and Figural After-Effects. On the assumption that normalization transfers fully whereas satiation effects are localized, it should be possible to distinguish the two processes by arranging a situation in which there is a relatively large distance between inspection and test figure. The relative importance of the two processes would then be given by the proportion of a continuous effect which remained in the transfer situation. Morant and Mikaelian (1960) found that two thirds of a contiguous tilt after-effect transferred over  $7^{\circ}$  of visual angle. Morant and Harris (in press) had their subjects adjust a line to be parallel with a vertical line  $14^{\circ}$  away. A tilted inspection line had previously been exposed in the same position as one of these test lines and the constant error in setting the test lines to parallel was taken as a measure of the satiation effect alone, on the assumption that the Gibson effect would transfer fully and thus affect both test lines equally whereas the satiation effect would be restricted to the contiguous test line. The obtained function of magnitude of effect against inspection line tilt was a good fit to the predicted curve for

the Köhler effect.

Finally, the fact that visual inspection of a tilted line appears to produce a negative after-effect on the tactile-kinaesthetic vertical (Morant and Mistovich, in press; Silver and Morant, 1962) suggests that a psychophysical theory is more likely to encompass all the facts than a model tied to specific neurological processes.

It seems reasonable to conclude, from all the evidence cited, that there are at least four perceptual mechanisms which can induce an apparent change in the tilt of the field of view. These are;

(a) Gibson-type adaptation in which the inspection of lines off the main axes causes a local shift in the whole subjective dimension of tilt of at most a few degrees. (b) Perceptual accommodation to even large displacements of the visual frame of reference. This mechanism may be of two kinds, one dependent on active learning and the other not. (c) Simultaneous contrast of direction of a few degrees, seen when a line is superimposed on a background of lines running in a different direction. (d) A figural after-effect in which acute angles tend to look larger by a few degrees after one of their arms has been inspected.

Apart from all these mechanisms, there is a further obvious possible cause of normalization. Ogle (1950) suggested that it could be due to the eyes rotating about the visual axis (torsion) so as to keep the normally vertical retinal meridian parallel to the main lines of the field of view. This possibility will be discussed in the next section.

CHAPTER 2AN EXPERIMENTAL INVESTIGATION OF THE RELATION BETWEEN EYE TORSION  
AND TILT ADAPTATIONEye Torsion Defined.

An eye has no fixed axes of rotation. Therefore, in order to specify the movements of an eye geometrically, any one of several axis systems may be adopted. The choice is arbitrary; it is not a question of which is or which is not correct. However, for any particular purpose one axis system may have practical advantages. In the Helmholtz axis system the horizontal axis is assumed to be fixed to the skull, and the vertical axis is assumed to rotate gimble-fashion with the horizontal axis. The position of a short reference line on the eye is expressed in terms of elevation ( $\lambda$ ) and azimuth ( $\mu$ ). In the Fick system it is the vertical axis which is considered fixed, and the position of a short reference line is expressed in terms of latitude ( $\theta$ ) and Longitude ( $\phi$ ). The Fick system is simply the Helmholtz system turned to the side through  $90^\circ$ . In each system, rotation of the eye about the visual axis is known as torsion, although the baseline from which torsion is measured varies according to the axis system used.

Listing proposed that any movement of the eye could be regarded as having occurred about a single axis in the mid-vertical or equatorial plane (Listing's plane) of the eye (plane HD'ID in figure 6). For elevation and depressions of the eye this axis is the horizontal axis, for lateral movements it is the vertical axis, and for oblique movements the axis is between the horizontal and vertical axes. In other words, the axis of rotation in Listing's plane is at right angles to the plane containing the initial position and the final position of the visual axis (plane OPB in figure 6). Only one axis is assumed to exist in this system; it always lies in Listing's plane, but has no fixed position within that plane. The extent of such a movement is given by the angular separation of the initial and final positions of the centre of the pupil (i.e. the angle of eccentricity  $\Pi$  in the case of movements from the primary position); its direction is given by the angle which the meridian joining these two positions makes with an objectively vertical or horizontal meridian ( $\xi$  or K in figure 6).

It follows that if Listing's system is to provide a comprehensive description of an eye movement, then torsional rotations of the eye about the visual axis, with reference to the meridian along which the visual axis travels, must be assumed not to occur. Helmholtz called this "Listing's law".

FIG. 6 Diagrammatic representation of the geometry of eye movements. The direction of gaze is assumed to have moved from the primary position OB to an oblique position OP through an angle of eccentricity,  $\pi$ . The movement has occurred along the meridian BH which is at an angle K to the original horizontal meridian DBD, which is equivalent to it having occurred about axis XY in the equatorial frontal plane (Listing's plane). The horizontal marker (between the small vertical bars) initially makes an angle  $\delta 1$  with the meridian along which the visual axis moves and, according to Listing's law, this angle remains constant ( $\delta 1 = \delta 2$ ). The eye can also be regarded as having moved on Helmholtz's axes through an angle of elevation,  $\lambda$ , and an angle of azimuth,  $\mu$ . For angle  $\delta 2$  to remain equal to  $\delta 1$ , the eye (and marker) must ~~tert~~ turn through angle  $\rho$  relative to the final plane of regard DCD.

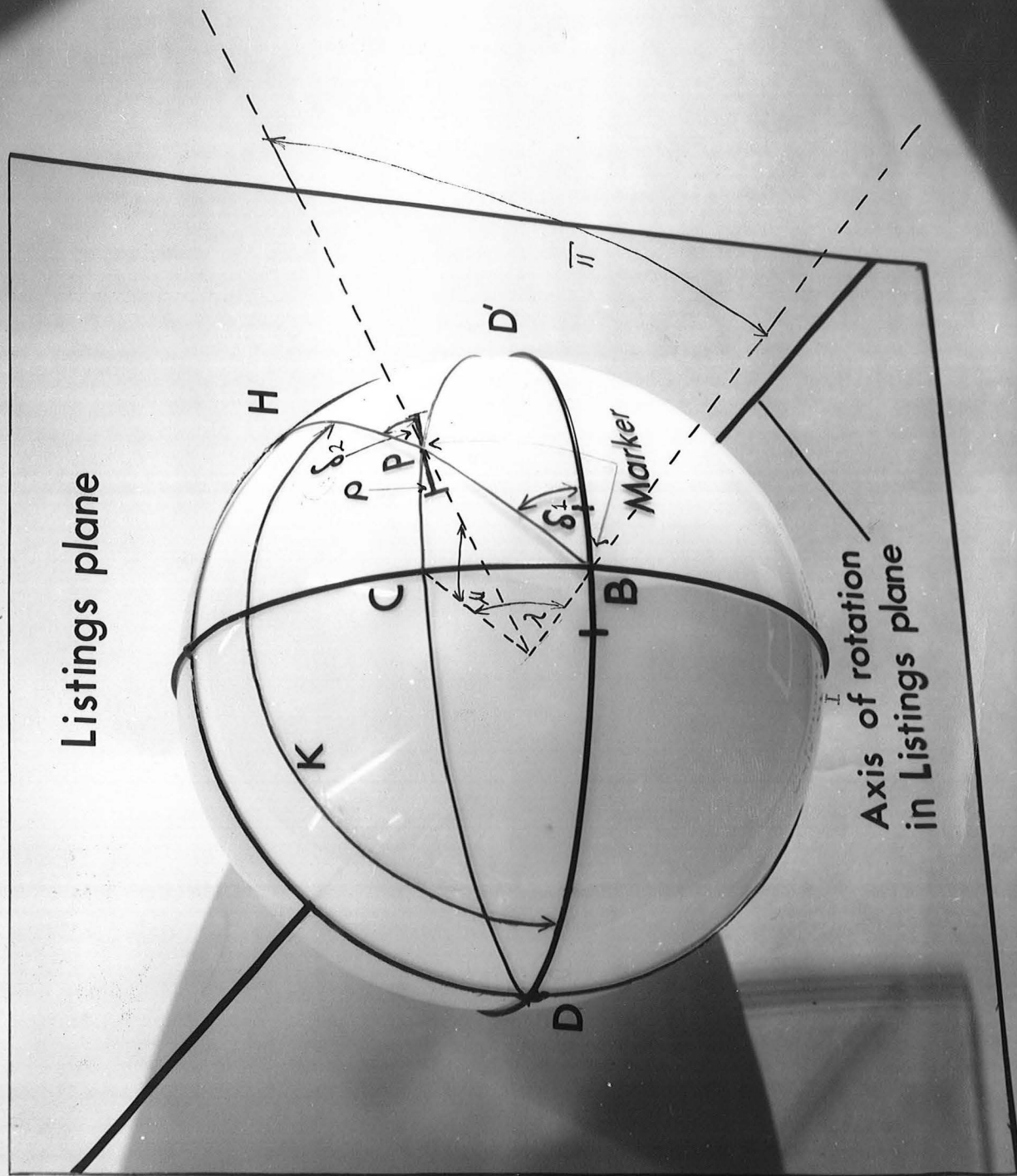


FIG. 6

If an initially horizontal, short reference line is substituted for the point marker then this assumption may be tested:  $\delta_1$  should always equal  $\delta_2$ . The assumption appears to be correct for the case of versions including oblique versions (Quereau, 1954). But it is only for such conjugate eye movements that Listing's law holds; when the angle of convergence between the eyes changes, torsion in Listing's sense, does occur (Allen, 1954).

If, on the other hand, movements of an eye are referred to either the Helmholtz or the Fick axis systems, the positions which a line marker assumes during oblique version movements can only be accounted for by assuming that torsion has occurred. But this means merely that torsion has been re-defined. Torsion on the Listing system is defined in terms of the angle  $\delta$  of figure 6, that is, the angle which a horizontal marker makes with the meridian along which the line of sight moves (BH). This remains constant according to Listing's law. Torsion on Helmholtz's system is the angle which the marker makes with the plane of regard (D"PD), that is, angle  $\gamma$ . In Fick's system torsion is the complement of angle  $\gamma$ . These angles ( $\gamma$  in figure 6, or its complement) are a function of the angle  $\delta$  and the angle of eccentricity ( $\parallel$ ) and are not constant according to Listing's law. Clearly, also, these systems can encompass torsion which occurs without any change in the position of the visual axis, whereas Listing's system cannot.

In general, then, a one-axis system, such as Listing's, can encompass only two types of eye movement; whether torsion is obtained in a given situation depends on the meridian with respect to which torsion is defined, and on the particular axes used in the system (see table 2).



Donders' law originally stated that the torsional position of the eye, depends only on the direction of gaze. Donders revised his law when he became persuaded by his assistants that torsional eye movements occur when the head tilts. Donders' law is now taken to mean that the torsional position of the eye in whichever system it is defined is independent of the manner in which the eye is brought to a particular position.

Torsion, as defined in any of the systems mentioned, is known to occur in many circumstances. These circumstances are listed in table 2. Of these, only optokinetic torsion is relevant to tilt adaptation. Optokinetic torsion is induced by visual lines rotating in the frontal plane.

Brecher (1934), using both an after-image method and direct viewing of the eyes, showed that the eyes undergo nystagmic torsional jerks of a few degrees' amplitude when fixating a rotating sectorized disc. Noji (1929) used the after-image method, and found that his own eyes torted in response to a rotating line. This tortional response of the eyes is analogous to the horizontal nystagmus produced when vertical lines moving horizontally are inspected. The tilt after-effect, however, is produced by the inspection of a stationary tilted line, and therefore my task was to investigate whether inspection of such a line induces eye torsion. My second purpose was to use my method of measuring eye torsion, which is objective, and more accurate than the methods used by Brecher and Noji, to check their claim that rotating visual patterns induce eye torsion.

#### The Measurement of Eye Torsion

Methods of measuring eye torsion are either subjective and depend on



Name	Inducing Conditions	Listing's Law
Oblique gaze torsion	Function of meridian of movement and eccentricity	Holds
Countertorsion	Head Tilt	Does not hold
Opto-kinetic torsion	Visual patterns rotating in frontal plane	
Cyclofusional torsion	Torsional disparity	
Cyclophoric torsion	Release from cyclofusion	
Convergence torsion	Convergence of lines of sight	
Spontaneous fluctuations of torsion	Unknown	

TABLE 2 Types of eye torsion and their inducing conditions

judgments made by the subject, or are objective and are independent of the subject's judgments. Subjective methods will be discussed first.

The After-Image Method. In this method an after-image of a line of light is formed. Any torsion which occurs while the after-image is visible will show itself as a tilting of the after-image relative to an objective reference line. Ruetes (1848) first used this method, which was later developed by Donders (1870), Mulder (1874), Fischer (1930), and McCord (1953). Subjects require a lot of practice in order to use this method. It has never been validated against an objective measure of torsion but it is unlikely to be accurate to more than about one degree.

Mapping the Blind Spot. Closely related to the after-image method is the procedure in which torsion is measured by the angular position of the blind spot relative to the fixation point. The method was first used by Tourtual (1840) and further developed by Nagel (1896), Mulder (1897), and Quereau (1955). The method demands very steady fixation and is not likely to be any more accurate than the after-image method.

The Maddox-Rod Test. This is used clinically as a test for cyclophoria and as such is essentially a method for measuring eye torsion. A vertical line is presented to one eye and a spot of light to the other. The amount by which the line must be turned in order to appear vertical is the measure of torsion in the eye which is viewing the line. It is well known (Gibson and Radner, 1937) that lines which appear off-vertical come to appear more vertical as they are inspected. This process will lead to an under-estimation of torsion as measured by the Maddox-rod test.

The Astigmatic Axis. Javal (1867) noticed that the direction of the axis of his cylindrical spectacles did not coincide with his astigmatic axis when his head was tilted sideways and he interpreted this as being due to eye torsion. Walton (1948) used this shift of the astigmatic axis of the eye as a measure of eye torsion. The method can only be used on highly astigmatic subjects. Nagel (1896) described a variant of the astigmatic axis method. He observed, in the dark, the radiant shape of a distant luminous point, produced by the astigmatism of the eye's lens. A thread, fixed to a spectacle frame, was centred on the luminous point and then rotated until it coincided with a recognizable ray of the astigmatic pattern, thus giving a measure of torsion. The accommodation mechanism was paralysed to eliminate possible effects of accommodation changes on the astigmatic ray pattern. This is a method which has not been used by others.

Cyclofusional Amplitudes. If two stereograms are rotated relative to one another, the angle through which binocular fusion is maintained is the cyclo-fusional amplitude and has been taken as a measure of eye torsion. This method is no longer used, for it has been shown (Ames, 1926) that the cyclo-fusional amplitude is to some extent a function of Panum's fusional areas. Several procedures have been proposed to overcome this difficulty.

Instead of measuring the angle at which fused images separate, Hofmann and Bielschowsky (1900) placed a horizontal line above the target in one eye and a similar line below the target in the other. The angle through which the stereograms could be rotated before the lines no longer appeared parallel was said to be a measure of cyclotorsion. Hermans (1943)

and Allen (1954) used Volkmann discs for their stereograms. These are rings each of which has a radius drawn on it in such a position that, when the rings are fused, the two radii can be adjusted to form a diameter. Subsequently, eye torsion is measured by the amount of rotation of the targets needed to restore the straight diameter. Similar methods have been used by Ogle (1946) and Harker (1960). These methods measure only the relative torsion between the two eyes. They are subject to errors due to normalization to the vertical.

All the subjective methods have the following limitations.

1. They involve the use of a visual stimulus as an integral part of the process of measurement. It is known that visual stimuli can induce torsion (Brecher, 1934; Noji, 1929; Howard, 1963). There is thus the possibility in all subjective methods that the stimulus used to indicate torsion will itself induce it.
2. No subjective method is capable of accurately measuring rapid changes or torsion.
3. It is impossible, using these methods alone, to dissociate the judgment variability of the subject from fluctuations in torsion.
4. It is not possible to allow for errors due to changes in fixation.
5. They provide, in themselves, no method of validation.

The only advantage they have is that they require very little instrumentation. As research methods, they have been entirely replaced by objective methods, but they may retain usefulness for clinical and demonstration purposes. Their reliability and validity could be checked

against an accurate objective measure of torsion.

The following are the objective methods

Direct Viewing. In the earliest methods (reviewed by Nagel, 1896) the experimenters measured the rotation of their own eyeballs by looking in a mirror at the movement of the iris, the conjunctival vessels, or marks applied to the conjunctiva. It has been repeatedly pointed out that the conjunctiva is not attached to the eyeball and therefore blood vessels or other marks on the conjunctiva are unreliable indicators of torsion. De Kleyn and Versteegh (1924) marked the cornea with a gelatin suspension; others observed the movement of the optic papilla through a retinoscope (Grahe, 1938).

The eye may be viewed through a telescope or low-powered microscope. Cross-wires in the eyepiece are centred on the pupil and aligned with the recognizable features of the iris (Loring, 1915; Brecher, 1934; Kompanejetz, 1928; Merton, 1956). In using this method I have found it very difficult to keep the cross-wires centred and to take readings. It is impossible to follow fast torsional movements. These same comments apply to the use of the ophthalmometer for recording the position of the astigmatic axis (Woinow, 1871; Walton, 1948).

The Use of Contact Lenses. Fender (1955) photographed the movement of a beam of light reflected off a small mirror which was attached to a contact lens so that it was parallel to the visual axis. He claimed to have recorded torsional movements down to a few seconds of arc. This method can record fast changes in torsion and does not depend so much on the skill of the observer as do the direct viewing methods. However, there is doubt on several points. Fender did not report how much of the recorded variation was due to head movements and instrument instability

His results in the seconds of arc range must have been partly due to such causes. The method depends on having the mirror parallel to the assumed axis of torsion, otherwise the record will be contaminated by other eye movements. The lenses are expensive and, for many subjects, uncomfortable, and they put a load on the eye. Finally, a contact lens lies on the conjunctiva and therefore may slip relative to the eyeball.

Davies and Merton (1958) overcame the difficulty of slipping lenses by using a smaller lens which was sucked firmly on to the cornea. A mica plate and mirror were mounted on the lens. The light was plane-polarized, then passed through the mica plate, reflected off the mirror and finally passed through a second nicol. The amount of light through the second nicol was a function of the angle through which the mica and eye had turned. This method gives an objective record, and can record fast changes of torsion. However, the authors give no indication of its accuracy. The load on the eye must be considerable and the mica plate would obstruct vision.

Photographic Methods. Photographic methods depend on having in the photograph some marker on the eyeball and some markers on the head. Brecher (1934) and Free and Jones (1959) used iris marks on the eye and, as head markers, the corners of the eye. Both these are very indistinct and the corners of the eye are not stable. Graybiel and Woellner (1958) sewed black silk sutures on the conjunctiva on each side of the cornea and stuck a piece of white plaster on to the skin near the eye to indicate the position of the head. This technique is very unsatisfactory; the conjunctiva is loose and so is the skin on the head.

Finally, Miller (1962) used iris marks to indicate the position of the

eye, and the edge of the film to indicate the position of the head. The measurements were made by superimposing projected images on a screen. He reported that the method had a precision of  $\pm 5.3^{\text{min.}}$  of arc, but did not indicate whether this represented the repeat reliability of his readings on a single slide or whether it represented the instrument's validity.

Electro-oculography cannot be used to register torsional movements of the eye, for such movements do not involve any movement of the eye's anteriorposterior electrical dipole.

The ideal method of recording eye torsion should be objective, accurate and convenient; it should be capable of recording rapid movements, should not introduce visual stimuli, and should depend on the minimum of theoretical assumptions. An indication should be given of the extent of the errors due to mechanical instability, reading inaccuracy, and loss of fixation.

The method which I devised to satisfy the above requirements involves photographing the fine episcleral blood vessels of the eye together with two head position indicators supported, one on each side of the eye, by a forked stem which in turn is attached to a rigid, hard-wax bite. The line joining kinks on two blood vessels defines one index line and the line joining the two head position indicators another index line. The angle between these two index lines is measured and is the relative torsion angle.

It is important that episcleral vessels are chosen and not conjunctival ones. Only the former are attached to and move with the eye-ball. The others, being in the conjunctiva, are attached indirectly to the eyelid (Duke-Elder and Wybar, 1961, p. 547). It is easy to distinguish between

them by observing the vessels when the conjunctiva is lightly moved with the finger. Most people have been found to possess suitable vessels.

Figure 7 shows the general lay-out of the apparatus used to photograph the eye. The lens of the original camera is replaced by an 8 in. focal length lens. The long focal length enables the camera to be kept well away from the subject. The eye-to-lens distance and the film-to-lens distance are both equal to twice the focal length of the lens. A minus-red filter is used to enhance the contrast between the blood vessels and the sclera. The lens is stopped down to increase the contrast and depth of focus. The camera is a focal-plane shutter type.

The camera and lens are mounted on an optical bench and accurately aligned with and centred on the pupil of the viewing eye. During the alignment process the eye is focussed and centred in a frame outline drawn on a ground glass screen. The film is placed in this image plane by using a gauge block and stop clamp. A small focusing adjustment screw is placed behind the camera body and a series of six photographs taken to find the best focusing position. The subject's head is very firmly supported by two temple clamps, one forehead clamp and a moulded chin rest.

A plate at  $45^{\circ}$  to the eye-camera axis conceals the camera from the subject and gives him a reflected view of any visual target which the experimenter may wish to expose.

Figure 8 shows the bite, which is made from dental base plates on a metal base and which goes back to the molars. Two fine black crosses are marked on the white plastic U-shaped piece and this is attached to the bite by a metal stem which can be bent until the crosses lie one on



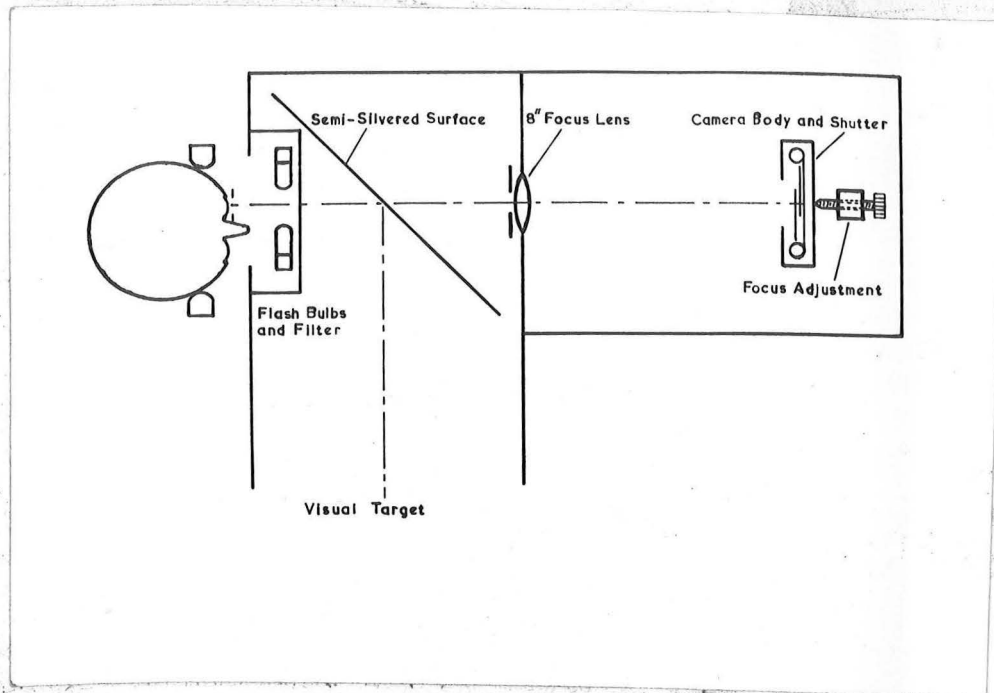


FIG. 7. The general lay-out of the photographic apparatus.

each side of the eye and as near as possible to the plane of <sup>the</sup> limbus.

Accuracy is increased by having the head position markers and episcleral vessel kinks as far apart as possible. This is one reason why iris marks are not preferred; the other reason is that they are less easily identified. However, it sometimes happens that the clearest episcleral vessels are near the limbus and one may judge these the best to use.

The stimulus field is dark, the duration of the flash being less than the reaction time of the eye movement reflexes.

The negatives of the 35 mm photographs are projected to a size of about 30 cm. The projector is equipped with two fine adjustments which enable the operator to deflect the projected beam from side to side or up and down. A slide is projected on the screen and the pupil is centred on this inner part of the screen (part B in Fig. 9). This centring is not critical. Fine pencil marks are made on the screen coincident with two recognizable kinks on the chosen vessels, which are symmetrical on a diameter through the pupil. These marks are joined by a fine, straight index line. The head-position indicators are pencilled in on the outer part of the screen (part A in Fig. 9). These are the reference indices for all the other slides of the subject. The reading on the torsion-angle scale is noted. The next slide is projected and the head position indicators are brought to exact coincidence with the reference marks by translating the picture and if necessary tilting the whole screen by turning a screw which supports one end of the screen (control 1 in Fig. 9). The vessel kinks are then aligned on the vessel index line by turning a control (control 2 in Fig. 9) which rotates only the inner part B of the screen and the pointer

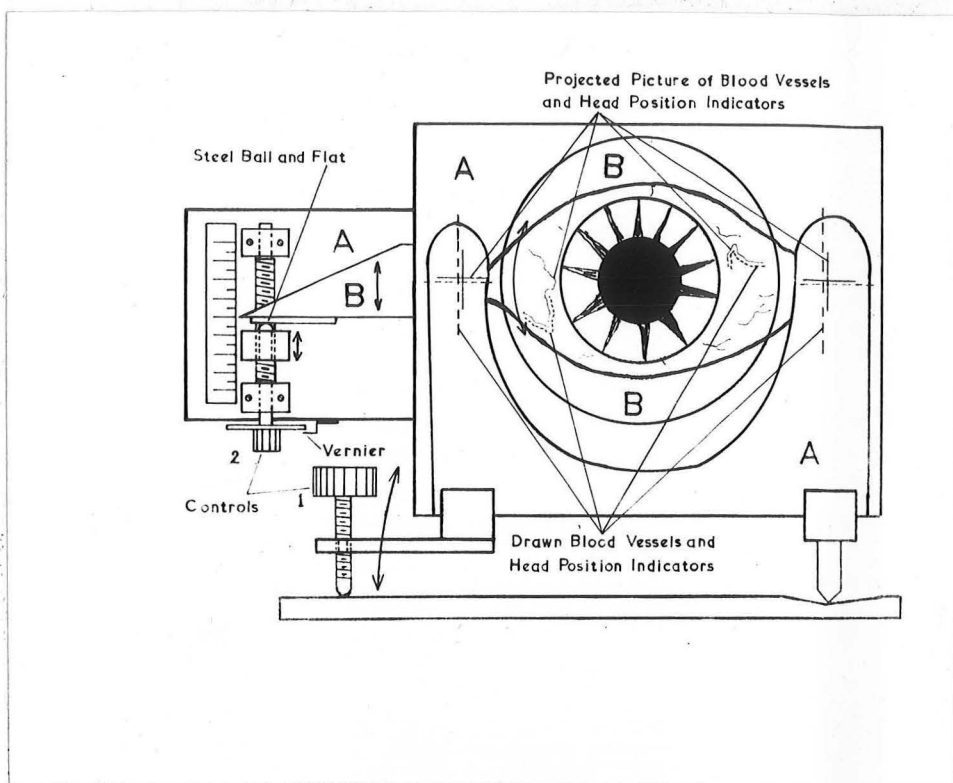


FIG. 9. The projection screen and torsion angle measuring device.

on the scale. If the eye has moved in its direction of gaze between the taking of the first picture and the second, the picture has to be translated as well as rotated to give coincidence of the vessel kinks and the vessel index line. The scale reading is now taken. The method of superimposing a negative and a positive slide was tried rather than the method of using index marks, but it was found that it was no more accurate and required a second projector and a semi-silvered mirror which had to be kept rigidly fixed.

Reliability and Validity. The difference between the scale reading thus obtained and the scale reading for the reference slide is the projected torsion angle, which is a measure of the relative torsion which has occurred between the two pictures. Possible sources of error are discussed below.

1. Reference Point Asymmetry. Care must be taken to use two kinks on the chosen blood vessels which are roughly equidistant from the pupil centre. If they are asymmetrical, any off-centring of the subject's eye at right angles to the blood vessel index line causes one kink to move further than the other, and this will give rise to an apparent tilting of the index line of the screen, for which allowance cannot be made.

2. Reading Variability. Individual differences in reading the slides were eliminated by having one person do all the readings on any one series; the order of the slides in the series was changed between sets of readings. The pairs of readings differed, on average, by  $0.07^{\circ}$ , or about  $4'$  of arc.

3. Movements of the Camera, Head and Bite. The edge of the film is not used as part of the measurement, so that it is not necessary to ensure that the

camera has a constant position relative to the subject, so long as the film is kept in focus and is in a position to take a picture of the objects required. Similarly, it does not matter that each slide is placed in the projector in exactly the same way. The method of putting all the information required for the measurements on the actual emulsion is based on well-established practice.

It is, however, necessary to ensure that the subject's head does not tilt (unless this factor is being studied). This is because the eyes are known to counteract partially as the head tilts. The efficiency of the head clamping system was tested by taking photographs when a subject alternately strained his head to left and right. No torsion was detected unless the head clamps were left deliberately loose. At first the head was anchored by means of the bite but it was found that any small head movements were not transmitted to the bite because the teeth are not rigidly held in the jaws. When the head was anchored independently of the bite, the bite was not under constraint and did not move relative to the head (and eye). The same small head movements would still occur but would not now be a significant source of error because countertorsion is only a fraction of the head tilt which induces it.

4. Instrument Instability. A small model eye was made with gimbal mountings to simulate the rotations of the eye and an axial movement to simulate torsion. Mock blood vessels were inscribed on it and head position indicators fastened to it. A series of photographs were taken with the model eye in the same position throughout. The resulting readings showed no detectable variation; that is, they did not vary more than a series of readings taken from a single slide.

Finally, as a check on the validity of the measure of eye torsion, the eye model was photographed in various positions of gaze relative to the camera axis and with various "torsion" angles imposed upon it. Corrected readings (see next section) closely matched the real torsion of the model eye, with an average deviation of the same order as that obtained from repeated readings from one slide.

5. The Torsion Axis and the Spherical Correction Factor. I have adopted the recommendation of Fry et al. (1947) and used the Helmholtz axis system. Torsion is then defined as rotation of the eye about the visual axis in an assumed spherical eye. Torsion about this axis is measured with reference to the vertical axis of the Helmholtz axis system. For practical purposes it is assumed that the visual axis passes through the centre of the pupil.

It is now necessary to consider whether the measurements which I get from the photographs by the operations I have described give a direct measure of torsion as defined. If the direction of gaze alters between two photographs, the possibility exists that a correction factor will have to be applied, because spherical movements are being measured on a plane. The term "false torsion" is sometimes used in this connection but the term is ambiguous and will not be used here. The extent of the correction depends on the degree of off-centring of the eye, on the angle between the vessel index line and the direction in which the off-centring has occurred and on the axis system. For a Helmholtz system, where the torsion angle is small and the vessel index line is horizontal,  $5^{\circ}$  of oblique gaze require a correction factor of only a few minutes of arc.

Thus it is safe to assume that in experiments where the subject's visual axis is always at right-angles to the plane of the film, the readings on the instrument are a direct measure of eye torsion. The following is a rigorous statement of the rationale underlying the measuring technique and of the transformation from photographic projection to Helmholtz axes.

Definitions. (a) Torsion,  $T$ , is the angle of rotation of the eye about the third Helmholtz axis. It is measured clockwise from the subject's viewpoint, in degrees from the top vertical.

(b) Projected torsion,  $t$ , is the angle of rotation of the projection of a short, straight marker on the surface of the eye on to a frontal plane. It is measured from the operator's viewpoint, anti-clockwise in degrees from the top vertical. A vertical is selected for zero because  $T = 0$  transforms to  $t = 0$  for all angles of gaze.

The Transformation. Calling the Helmholtz co-ordinate of altitude  $\lambda$  and of azimuth  $\mu$ , then the transformation of a torsion measure from plane projection to Helmholtz axes is given by:

$$\tan t = \frac{\cos \mu}{\cot T \cos \lambda - \sin \mu \sin \lambda} \quad (1)$$

for all angles of gaze. To find  $\lambda$  and  $\mu$  from the projection, measure  $x$  and  $y$ , the co-ordinates of the marker on rectangular axes through the projected eye centre; then

$$\sin \mu = x/r \quad (2)$$

$$\sin \lambda = \frac{y}{r \cos \mu} \quad (3)$$

where  $r$  is the radius of the projected eye.

In practice, the marker is not short; the blood vessel index line is equivalent to a short marker only if  $T$  and  $t$  are referred to the centre of the line and the projection of the line respectively. To find  $\lambda$  and  $\mu$  for this centre, measure  $x_1, y_1, x_2, y_2$ , for the two index points;

then  $r'$ , the effective radius at this centre =  $r \sin \theta$  (4)

where

$$\theta = 1/2 \left[ 180^\circ - \left\{ \sin^{-1} \frac{\sqrt{(x_1^2 + y_1^2)}}{r} + \sin^{-1} \frac{\sqrt{(x_2^2 + y_2^2)}}{r} \right\} \right] \quad (5)$$

Taking

$$x' = 1/2(x_1 + x_2), \quad y' = 1/2(y_1 + y_2) \quad (6,7)$$

substitute  $x', y', r'$  in (2) and (3) above to find  $\lambda$  and  $\mu$ . This holds for all angles of gaze in the hemisphere, the index points being assumed symmetrical. For small deviations,  $x'$  and  $y'$  used with uncorrected  $r$  give a good approximation. A narrow angle photograph is here taken as sufficiently close to normal projection.

The details of this technique have been published (Howard and Evans, 1963).

#### General Experimental Procedure.

The general procedure in the experiments was to take successive pairs of readings, one control and one test, separated by exposure of the inducing stimulus. The difference between a control reading and its accompanying test reading constituted a single determination of the effect of the stimulus.

The means of samples of between nine and twelve such determinations had standard errors of less than  $0.1^\circ$ ; with samples of this size, therefore



effects of about  $0.125^\circ$  reach the 0.05 (one-tailed) level of significance and there is a probability of 0.87 of detecting a true difference as large as  $0.2^\circ$  and a near-certainty ( $p > 0.999$ ) of detecting one as large as  $0.3^\circ$ .

The visual stimulus was a 12 in. x  $1/4$  in. vertical line of light with a small fixation point at its centre. Nothing else was visible. The line was seen reflected in a semi-reflecting surface; the camera was directly behind this surface, out of view. The line was 40 in. distant and appeared to the subject to be positioned with its centre straight ahead.

In the first series of experiments, the variables studied were: binocular versus monocular viewing; direction of tilt of the line:  $10^\circ$  left tilt, upright, and  $10^\circ$  right tilt in the frontal plane. The centre of the line was inspected for 10 sec. before the photograph was taken. On any one trial the line was alternately exposed to the left, upright and to the right, keeping the other conditions constant. In the binocular versus monocular viewing trial, the line was kept vertical. A trial usually consisted of either nine or eighteen determinations with intervals of about 30 sec. between determinations. Two male subjects between the ages of 25 and 35 were used in the first series of experiments. Both subjects had their tilt after-effect measured, using a constant stimulus method, and with conditions identical with those in which the photographs were taken. None of the subjects had need of any visual corrections.

It may be that if eye torsion occurred there would be an apparent change in the angular position of a line. It is not easy to turn the eye in its socket from outside, but we can utilize the cyclophoria that most people exhibit. Cyclophoria is the torsion an eye undergoes when relieved from cyclofusional reflexes induced by binocular corresponding visual targets. It is measured by recording any change in the torsion of an eye consequent on covering or closing the other eye. This change was measured on one subject, and any related shift in the apparent vertical position of the line.

In the second series of experiments, the same line of light was used but was seen rotating about its centre in the frontal plane. The variables studied were: amplitude of rotation at the time the photograph was taken, starting at the vertical position (various angles between  $2^{\circ}$  and  $80^{\circ}$ ); starting position of the line ( $4^{\circ}$ ,  $8^{\circ}$  and  $12^{\circ}$  off-vertical) with the photograph taken when the line reached the vertical position. In all conditions interspersed control readings were taken with the line stationary at the starting position.

## RESULTS

### First Experimental Series


Neither of two subjects showed any evidence of a significant mean change of the torsional position of the eye that could be related to the angular position of the stimulus line (Tables 2a and 2b). If any effect existed it must have been less than  $0.2^{\circ}$ . Both subjects revealed a tilt aftereffect of approximately  $2^{\circ}$ , in response to 10 sec. inspection of the same line tilted to  $10^{\circ}$ . It is therefore concluded that eye torsion is not

Trials	Tilt of line in frontal plane		
	10° ↷	0°	10° ↶
1	1.1	0.9	1.0
2	1.4	0.8	0.6
3	1.0	1.2	1.4
4	1.2	1.7	1.5
5	1.6	2.4	1.9
6	1.9	1.5	2.4
7	2.6	1.5	1.5
8	2.0	1.9	1.7
9	1.2	1.2	1.6
Mean	1.55	1.45	1.5

TABLE 2a - Torsion as a function of tilt of line to 0°, 10° ↷, and 10° ↶ in frontal plane. Subject I.P.H.

Trials	Tilt of line in frontal plane		
	$10^\circ \curvearrowright \downarrow$	$0^\circ$	$10^\circ \downarrow \curvearrowright$
1	0.58	0.36	0.28
2	0.52	0.4	0.33
3	0.40	0.42	0.26
4	0.28	0.50	0.46
5	0.10	0.06	0.02
6	0.14	0.22	0.11
7	0.42	0.04	0.03
8	-0.19	0.01	0.12
Mean	0.32	0.25	0.2
$\sigma$	0.23	0.18	0.14

TABLE 2b - Torsion as a function of tilt of line to  $0^\circ$ ,  $10^\circ \curvearrowright \downarrow$   
and  $10^\circ \downarrow \curvearrowright$  . Subject F.T.

Trial	Degrees of  Torsion	
	Monoc.	Binoc.
1	1.5	0.45
2	1.25	0.22
3	1.33	0.03
4	1.73	0.93
5	1.85	1.53
6	0.98	0.62
Mean	1.44	0.8
$\sigma$	0.3	0.45


Mean diff. =  $0.64^\circ$  of  torsion with monocular viewing  
 $t = 2.78$   
 $p < 0.02$

TABLE 2c - Alternating monocular and binocular view of vertical line.  
 Subject I.P.H.


the cause of the tilt after-effect in conditions where the inspected line is stationary.

The left eye, viewing alone, was found to have a mean torsional position  $0.64^\circ$  anticlockwise of its mean position when both eyes were open (Table 2c). This difference is significant ( $p > 0.02$ ). The apparent angular position of a vertical line, with monocular and with binocular viewing, showed a similar shift in the opposite direction. This last experiment was on only one subject, but it does suggest that, although a tilted line does not induce torsion, torsion does cause an apparent shift in the position of a line.

### Second Experimental Series

This series of experiments was conducted with a line seen in rotation. A preliminary experiment on one subject revealed that of the three speeds of rotation,  $4/5^\circ$ ,  $3^\circ$ , and  $8^\circ/\text{sec}$ , the one inducing the most torsion was  $3^\circ/\text{sec}$ . This speed was therefore used in all subsequent experiments. Three subjects were tested at this speed, and at various amplitudes of rotation. The results are set out in Tables 2d, 2e, and 2f, and in Fig. 1. Two subjects showed significant amounts of torsion for amplitudes of  $6^\circ$  rotation, <sup>one subject for  $2^\circ$  and over.</sup> The amount of torsion varied roughly with the logarithm of the amplitude of rotation. There can be no doubt, therefore, that eye torsion is induced by a rotating visual line. The maximum effect obtained was  $1.4^\circ$  for one subject. The subject showing most torsion was tested with a line rotating to the vertical from  $4^\circ$ ,  $8^\circ$ , and  $12^\circ$  off-vertical (see Table 2g). The torsion was not significantly different from that induced by a line rotating the same amount from the vertical

Trials	Final angle of tilt															
	1°	1.5°	2°	3°	4°	6°	8°	10°	12°	14°	16°	20°	24°	30°	36°	60°
1	0.16	-0.22	0.48	0.48	.99	0.58	0.38	2.1	0.88	0.66	-0.1	0.84	0.12	0.54	1.28	2.56
2	-0.38	0.54	-0.12	0.4	1.07	1.42	1.08	0.5	1.02	0.54	1.0	0.48	0.66	1.86	1.38	0.96
3	-0.14	0.34	0.34	0.2	0.06	1.22	0.74	1.2	0.32	0.86	0.2	0.54	0.16	1.56	1.44	1.66
4	0.32	0.22	0.22	0.12	0.75	0.68	1.14	2.5	0.94	0.96	1.2	1.2	1.24	1.30 0.88	1.52 1.40	0.18
5	-0.28	0.0	0.3	1.3	0.81	0.84	0.88	0.78	0.26	0.48	1.94	0.18	0.4	2.0 0.5	1.12 1.46	1.28
6	0.2	0.56	0.2	0.14	0.61	0.34	0.78	-	0.80	1.12	0.42	1.28	0.5	-0.9 0.18	1.58 0.10	-
Mean	0.02	0.24	0.22	0.44	0.71	0.85	0.83	1.4	0.70	0.78	0.6	0.76	0.51	0.96	1.26	1.32
$\sigma$	0.4	0.24	0.22	0.22	0.34	0.36	0.28	0.77	0.4	0.25	0.68	0.34	0.44	0.72	0.44	0.79
p	NS	0.1	0.1	0.01	0.01	0.01	0.001	0.01	0.02	0.001	0.1	0.01	0.05	0.01	0.001	0.02

TABLE 2d - Torsion induced by line rotating  at 3°/sec from the vertical. (Each entry is the difference between torsional position of eye at 0° and at the final angle of tilt).  
Subject: I.P.H.

Trials	Final angle of tilt							
	1°	3°	4°	6°	12°	20°	30°	80°
1	0.18	0.64	0.34	0.08	-0.10	0.28	0.82	0.1
2	-0.22	-0.08	0.78	-0.32	0.40	0.8	0.32	0.48
3	-0.18	-0.08	0.16	0.48	-0.08	0.18	1.22	0.4
4	0.9	0.2	0.08	0.42	0.40	0.82	-1.24	0.92
5	-0.6	-0.28	-0.01	0.26	0.74	0.2	-0.2	0.56
6	0.38	-0.22	0.28	1.12	0.08	0.44	0.08	0.4
7	0.78	-0.1	0.12	0.34	0.08	0.08	0.52	-0.16
8	0.22	-	1.22	0.58	0.62	0.68	0.92	0.6
9	-0.01 -0.32	-	-0.42	0.42	0.68	0.40	0.64	0.66
Mean	0.12	0	0.26	0.42	0.32	0.44	0.34	0.44
$\sigma$	0.6	0.3	0.45	0.36	0.33	0.26	0.63	0.4
P	NS	NS	NS	0.02	0.05	0.01	NS	0.02

TABLE 2e - Torsion induced by line rotating  $\sqrt{}$  at 3°/sec. from the vertical.  
 (Each entry is the difference between torsional position of eye  
 at 0° and at the final angle of tilt).  
 Subject: W.B.T



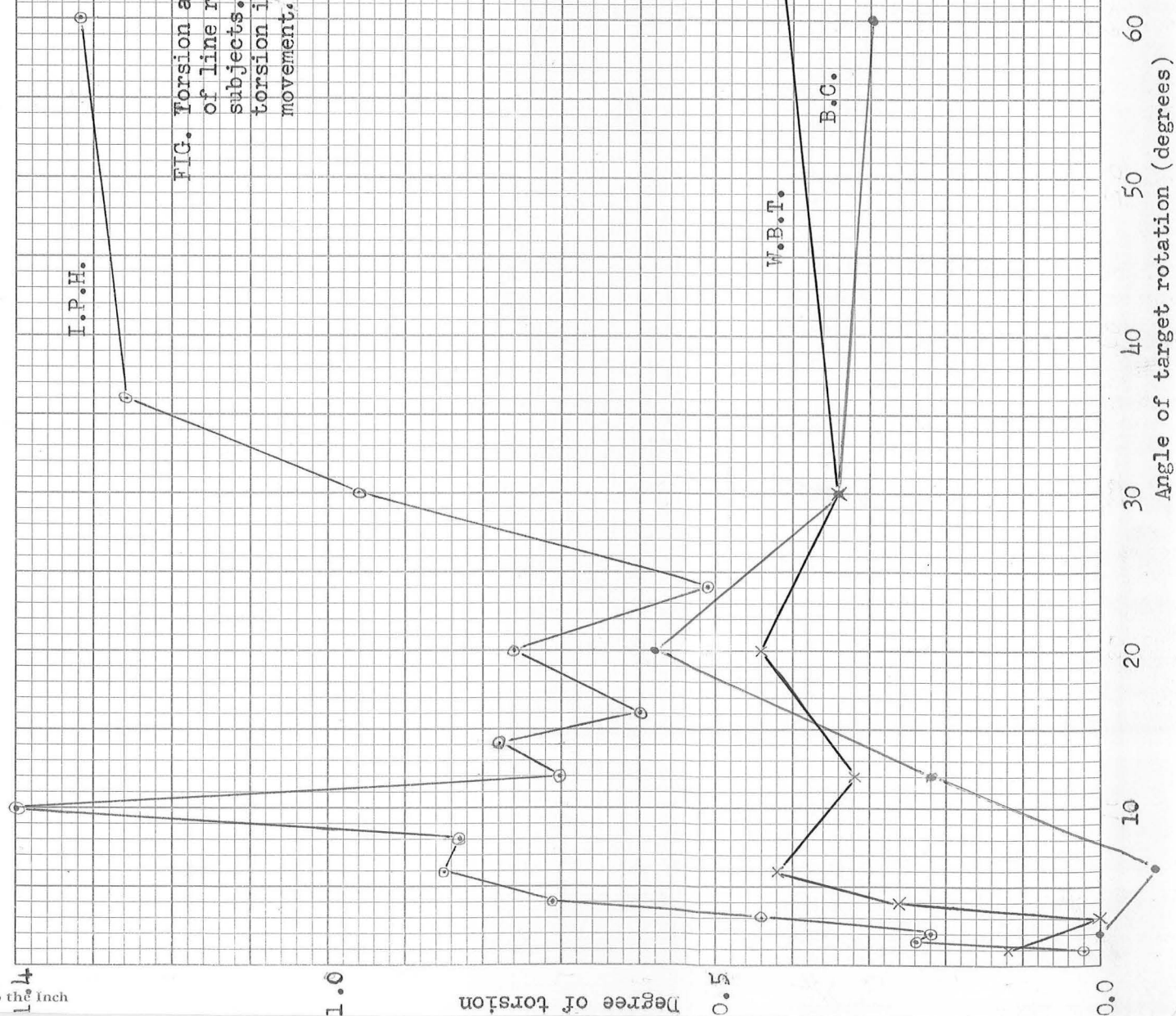
Trials	Final angle of tilt					
	3°	6°	12°	20°	30°	60°
1	0.56	0.4	0.48	0.18	-0.1	-0.16
2	0.0	-0.14	0.48	1.22	0.84	-0.14
3	-0.02	-0.14	0.04	0.68	0.02	-0.16
4	0.52	-0.86	0.42	0.38	0.38	1.02
5	-0.12	0.2	0.26	0.92	0.22	0.18
6	-0.06	0.16	0.36	-0.04	0.22	0.42
7	-0.44	0.12	-0.12	1.0	0.62	0.50
8	0.06	0.16	0.14	0.32	0.26	0.76
9	0.66	0.12	-0.06	0.60	0.6	0.36
Mean	0	-0.06	0.22	0.58	0.34	0.3
$\sigma$	0.32	0.33	0.33	0.36	0.26	0.38
p	NS	NS	0.1	0.01	0.01	0.1

TABLE 2f - Torsion induced by line rotating  $\sqrt{}$  at 3°/sec from the vertical.  
 (Each entry is the difference between torsional position of eye  
 at 0° and at the final angle of tilt).  
 Subject: B.C.

Trial	Initial angle of tilt		
	4°	8°	12°
1	0.76	0.66	1.12
2	0.58	0.64	1.04
3	0.72	0.42	1.02
4	1.12	1.46	0.50
5	0.68	0.54	0.40
6	0.38	0.54	1.22
Mean	0.71	0.71	0.88
$\sigma$	0.3	0.5	0.34
p	0.01	0.05	0.01

TABLE 2g - Torsion induced by line rotating  $\sqrt{\quad}$  at 3°/sec. to the vertical from a tilt of 4°, 8°, and 12°.  
 Subject: I.P.H. The mean values are not significantly different from the corresponding values in Table 2d.

FIG. Torsion as a function of amplitude of tilt of line rotating at 3°/sec for three subjects. Positive torsion angles indicate torsion in the direction of the target movement.



position. Optically induced torsion is therefore related to the rotation of visual objects rather than to the direction of rotation relative to the vertical.

### DISCUSSION

In answer to Ogle's suggestion, it can now be stated that optically driven eye torsion cannot explain the after-effect of inspecting a stationary tilted line . This conclusion conflicts with that of Greenberg (1960), who concluded that eye torsion is induced by observation of a tilted figure. His figure was a frame tilted  $28^{\circ}$ , and he measured torsion by aligning a rod with an after-image. He recorded torsion of several degrees, i.e. of roughly the same angle as the extent of the apparent displacement of the vertical position of the test rod. This was a different inducing stimulus from the one I used, and the after-image method of measuring eye torsion has not been validated. He used a moving line of light in his procedure and this would, to some extent, contaminate his results, although he claimed that the moving line alone did not have the same effect as when the stationary tilted frame was added. More measurements using an objective technique on a variety of inducing stimuli need to be done before these apparently conflicting results can be resolved. However, it may be concluded from my study that the tilt after-effect can arise in a situation where there has been no shift of the mean torsional position of the eyes.

The results of the second experiment confirm the results of Brecher and Noji. A rotating visual display induces eye torsion in the same direction

The maximum effect of  $1.3^{\circ}$  is much less than the effects reported by the other workers. My records show that the eye undergoes spontaneous torsional movements of over one degree. Furthermore, it is likely that optical induced torsional movements are nystagmic, as are the analogous optogyrar lateral eye movements. The variability of control and test readings was compared, using pooled estimates from a sample of sets of determinations in which the inducing stimulus rotated  $60^{\circ}$  or  $80^{\circ}$ . The readings taken before rotation of the stimulus had a standard deviation of about  $6^{\circ}$ ; those taken after, a standard deviation of about  $10.5^{\circ}$ . The difference between these measures is significant at the 1% level, and represents, I suspect, an increased amplitude of torsional nystagmus due to the rotating target. My results represent the mean amplitude of the torsional movements, those of Brecher and Noji probably represent the maximum amplitude of the movements. In any case their rotating visual target was more complex than mine.

The results show that movement towards and movements away from the vertical have the same effect, and this result strengthens the conclusion that torsional eye movements do not represent an attempt by the eye to keep the main lines of the visual field on the normally vertical retinal meridian.

CHAPTER 3AN EXPERIMENTAL ANALYSIS OF A NORMALIZATION PROCESS IN THE JUDGMENT OF  
RELATIVE DEPTH

In a study of reversible perspective in three-dimensional objects (Howard, 1961), it was hypothesized that steady fixation of objects at different relative depths would lead to a disruption of relative depth perception. A search of the literature revealed very few papers on the effect of long fixation on relative depth perception.

Köhler and Emery (1947), in their work on figural after-effects in the third dimension of visual space, were the first to mention the possible effects of steady fixation on relative depth perception. In their first experiment they presented an inspection (I) object in the frontal plane. A test object was subsequently shown in the same location turned through  $25^{\circ}$  or  $45^{\circ}$  backwards or  $25^{\circ}$  or  $45^{\circ}$  forwards. Each time, the T or test object appeared as if displaced from the frontal position of the I-object. In a second experiment they showed that after fixation of a concave I-figure, a flat T-figure appeared convex. Monocular viewing was said to reduce these after-effects substantially. In a third experiment they showed that T-objects always recede from I-objects. Thus T-objects behind the position of a preceding I-object were pushed backwards and T-objects in front were pushed forward. These opposed effects on the T-object, it was argued, exclude the possibility that after-images cause the T-objects to appear dimmer, and to recede because of this. Up to a point, the extent

of the effect of the I-figure was found to increase as its distance from the T-figure increased. This distance paradox was said to be analogous to the one found for two-dimensional figural after-effects.

Köhler and Emery (1947) discussed the possibility that the three-dimensional after-effects may be reduceable to after-effects in two dimensions. They pointed out that a test figure, having a different position in depth to an I-figure, will project images to each eye at least one of which must have a slightly different retinal position to the corresponding I-figure. This should cause the T-image or images to retreat from the positions occupied by the I-figures and these shifts could be interpreted by the subject as a change in the binocular disparity, and hence the three-dimensional position, of the T-object. In outlining this argument Köhler and Emery admitted its logical validity but claimed to have refuted it by an experiment. In this they presented, by means of a stereoscope, the left-and right-eye views of the I-figure alternately. This was said to destroy the three-dimensional appearance of the I-figure; but to leave a two-dimensional pattern which would reveal any purely two-dimensional, ordinary figural after-effect which this pattern of stimulation may have been producing. Köhler and Emery did not find any after-effect after this procedure and concluded that the occurrence of three-dimensional after-effects depends on the three-dimensional appearance of the pattern.

Köhler and Emery did not report their procedure in sufficient detail to show whether they were successful in eliminating the three-dimensional appearance of the I-figure; it is my experience that stereoscopic vision may persist down to four alternations a second. Even if they did

eliminate it, they should still have got a two-dimensional after-effect on the basis of their own argument. Three subjects only were used in their experiments, and there has been no independent confirmation of their results.

Bergman and Gibson (1959) claimed to have demonstrated an after-effect of fixating a surface slanted in the third-dimension, which was not a figural after-effect. The stimulus was a textured surface, slanting at various angles either backwards or forwards. This was viewed through a tube so that no contours were visible. After 4 min. inspection, the subject was asked to set a similar textured surface to the subjective vertical. They found that the subjective vertical was displaced towards the I-figure. They suggested that this effect could not be due to figural after-effects because there were no contours in the I-figure. This is not a convincing argument, for the textured surface must have involved a density gradient in a fine pattern and there is no reason why a Köhler type satiation process should not occur differentially over such a surface.

Bergman and Gibson found that the effect was nearly as strong when the I-figure was not steadily fixated. They used this result to support the theory that the adaptation effect is not specific to the locality of the retina stimulated. This conclusion seems ill-founded; the extent of eye movements was not stated. A better test of whether the effect is locus specific would have been to expose the I-figure in one retinal locality and the T-figure in another.

Ogle and Weil (1958) studied the effect of duration of the stimulus



on stereoscopic acuity. They found a four-fold decrease in stereoscopic acuity associated with a decrease in duration of exposure from 1 sec. to 1/124th sec. They explained their results in terms of the number of extent of the eye movements during exposure.

Lit (1959) studied the effect of fixation conditions of stereoscopic acuity using the Howard-Dolman apparatus. He had three conditions of fixation. Condition 1 involved steady fixation of the movable comparison rod, condition 2 involved steady fixation of the immovable standard rod, and in condition 3 the subjects were allowed to fixate either at will. Condition 2 produced the lowest precision and condition 1 the best. In all conditions there was a movable comparison rod; the subjects never fixated a constant arrangement of rods. The results of Lit's experiment are therefore not directly related to the present investigation, but it is of interest to note that in his condition 2 where the subjects most nearly approximated to constant fixation of a fixed pattern, the stereoscopic acuity was worst.

Ditchburn and Pritchard (1960) studied binocular rivalry with two stabilized retinal images. Their findings do not relate to the problem of stereoscopic acuity and are of no concern here, but the technique is potentially useful for investigating the effects of constant fixation on depth discrimination.

Kunnapas (1960) investigated the psychophysical functions relating objective to subjective distance. He concluded his paper with the statement, "It is conceivable that, in analogy to adaptation to light intensity, temperature, etc., and adaptation of the subjective range to the stimulus range may change the exponent" (i.e. the exponent of the

psychophysical function). Künnapas gave no experimental evidence for this statement, but it does foreshadow our own results.

### Experiment I

Constant fixation of a three-dimensional pattern may have several effects on stereoscopic vision. Four possibilities are listed below.

Hypothesis A: Stereoscopic fatigue. The continued fixation of a pattern having depth leads to a deterioration of stereoscopic vision for that particular pattern in that particular locality, or a general stereoscopic fatigue of the whole field. In a task demanding an equality setting of distant rods, stereoscopic fatigue would cause an increase in the variance of the settings but no shift of the P.S.E.

Hypothesis B: Stereoscopic inversion. After long fixation of a three-dimensional pattern, the central mechanism of vision confuses the inputs from the two eyes. This confusion of the inputs leads to an inversion of the binocular disparities, such as occurs in a pseudoscope. In the absence of strong cues to the contrary, things would appear to be inside-out.

Asher (private communication) has claimed that normal stereopsis may be produced by alternating the two stereoscopically disparate views of a scene to the same eye in rapid succession. This finding suggests that the C.N.S. is indifferent to the ocular origin of disparity information, and if true would make our hypothesis more plausible.

Hypothesis B, if true, would lead to the same results as stereoscopic fatigue. Both mechanisms could be localized or general in their effects on the test stimulus, and in either case would lead to an increase in the region of uncertainty, that is, a decrease in the slope of the psychometric

function.

Hypothesis C: Normalization to equidistance. After fixating a three-dimensional pattern there is a shift of the norm of equidistance in depth such that the pattern comes to look flat. A corollary is that the relative distance of other three-dimensional patterns, occupying a similar retinal locality, will be judged in terms of the shifted norm of equidistance. There will be a general displacement of all relative distances in a direction opposite to the depth difference in the pattern originally inspected. This would be an adaptation or normalization effect, analogous to Gibson's normalization to the vertical (Gibson and Radner, 1937).

Hypothesis D: Three dimensional figural after-effect. This is based on Köhler's theory and states that test objects behind the position of a previously inspected object are apparently displaced backwards, and test objects in front are displaced forwards.

The following experiment goes some way towards testing these hypotheses.

Apparatus. There were two target patterns, an inspection pattern (I) and a test pattern (T). Each consisted of black cards arranged as in Figure 11. In each pair, the standard card remained stationary while the variable could be moved so as to be in front of, or behind the standard card. The lateral distance between the cards was constant; the cards were rigid, vertical and parallel to each other (figure 11).

The I and T cards were positioned in planes at right angles to each other and at  $45^{\circ}$  to a semi-reflecting mirror placed between them. The I and T cards were thus exactly superimposed when viewed from the subject's position, 9 ft. in front of the cards. Each standard card had a small hole

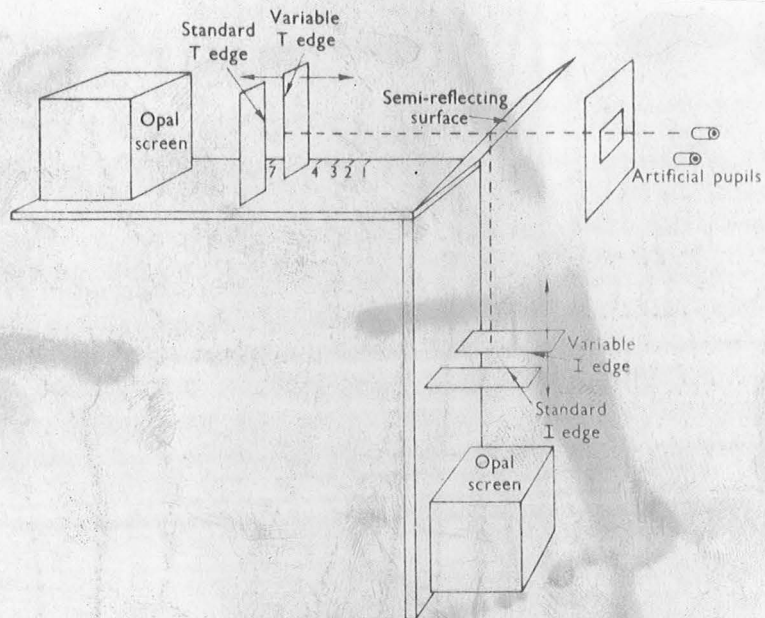


FIGURE 11

Apparatus used to demonstrate an adaptation effect in the judgement of relative depth.

near to its edge and these holes, which were also superimposed, served as fixation points.

An opal glass screen illuminated from the back was placed behind each pair of stimulus cards, which thus formed black-white vertical contours. The total appearance was that of a white rectangle, the left edge of which was the standard and the right edge the variable.

Each opal screen formed the front side of a 15 in. cubical box, on the back inner surface of which were mounted six, 60 watt, filament striplights. The surface illumination of the screen was 40 foot-candles. The two screens were matched for brightness in the following way; half of each was covered with black card so that the experimenter, sitting in the position of the subject, saw the two remaining halves side by side. Bulbs were removed from one of the light boxes until a match was obtained. A black screen was matched to the shade of black of the stimulus cards so that no contours were visible to the subject except the two inside edges of the stimulus cards.

Each variable card had a pointer attached to it, which showed the position of the variable on a scale marked off into five positions, each 2 in. apart. Figure 11 shows the arrangement of the five positions. A memory-drum exposure device presented to the experimenter a random series of the five position numbers, one at a time. The experimenter set the T card according to the number while the subject was viewing the I pattern. Electronic timers controlled the duration of exposure of the I and T patterns and the movement of the memory-drum device. The subject signalled his response to the experimenter by pressing a key backwards or forwards after each exposure of the T pattern.

Procedure. The subject was seated 9 ft. away from the target cards, with his head firmly clamped. Artificial pupils were used, the right-hand one being fixed so that the right eye of the subject was in line with the variable edges. The instructions to the subject were as follows. "You will see a white rectangle; keep your gaze centered on the small white spot on the left of the rectangle. The left-hand edge of the rectangle will be stationary; the right-hand edge will be moved so as to be in front of or behind the left edge. Indicate whether you think it is in front or behind by pushing this switch in the same direction. You will be given only 1 sec. to make this judgement, there will then be a period of 10 sec. in which you will see the rectangle or just a spot of light. Do nothing except fixate during this period. A warning click will be given just before each 1-sec. test period, there will be 50 tests alternating with 10-sec. intervals. The initial inspection period will be 2 min. Always respond 'in front' or 'behind'."

Each subject was given a practice session and then a session for each of four experimental conditions. The sessions were well spaced, and their order varied for the different subjects. The experimental conditions were as follows.

The equals condition. Here the I-pattern was the white rectangle with equidistant vertical edges. A 2-min. inspection period preceded the 50, 1-sec. test exposures interspersed with inspection periods each lasting 10 sec.

The disparity conditions. These were similar to the "equals" condition, except that the right-hand edge of the white rectangle was 2 in. in front of the left-hand edge in one condition and 4 in. in front in the other, during the inspection period.

The control condition. Here the I-pattern was a small fixation light only.

The test periods were brief so as not to disrupt the state induced

by the I-pattern. The 10 sec. reinforcements of the I-pattern were given to keep the effect "topped up". Each of the five positions of the variable edge of the test rectangle occurred 10 times in random order, making 50 readings in all. Each session occupied about 12 min.

Results. The raw data consisted of the number of responses in which the variable edge was judged "forward" of the standard edge. The total number of "forward" responses made by each subject in each condition was calculated, and the means of the five totals are shown in Table 4 for each condition.

An inspection of Table 4 suggests that fixation of a particular pattern with the variable edge in a forward position leads to a reduction in the number of forward responses, that is, to an apparent backward displacement of the variable stimulus in the test pattern. The estimated P.S.E.'s for each condition are also set out in Table 4 together with their standard errors. The results are in inches; positive quantities represent "forward" positions, that is, the variable edge appearing closer than the standard edge. The P.S.E.'s were obtained by averaging the 50 per cent. points (weighted two), the 75 per cent. points and the 25 per cent. points of the psychometric functions shown in Figure 12. An analysis of variance was done on the totals of "forward" responses and the results are set out in Table 5.

Tested against a standard error based on the residual variance from the analysis, the mean difference between the "equals" and 4 in. conditions yields  $t = 4.16$ , which for 48 degrees of freedom has  $p = 0.001$ . The mean difference between the 2 in. and 4 in. conditions gives  $t = 1.42$ , which is not significant. Hence the significant main effect of conditions is due

TABLE 4

## RESULTS FROM EXPERIMENT I

	Conditions			
	Control	Equals	2 in. forward	4 in. forward
Mean number of forward responses	25.6	25.8	12.8	15.6
$\sigma$ m. .. ..	3.61	1.80	1.96	2.36
P.S.E. .. ..	0.08	-0.05	3.08	2.18
$\sigma$ mdn. .. ..	0.78	0.37	0.51	0.44

TABLE 5

## ANALYSIS OF VARIANCE OF THE FORWARD RESPONSES FROM EXPERIMENT I

Source	d.f.	Sums of squares	Estimated variance	F	p
Conditions .. ..	3	140	46.7	16.2	<0.001
Stimulus categories .. ..	4	125	156	54.2	<0.001
Subjects .. ..	4	58	14.5	5.03	<0.01
Conditions x categories ..	12	50	4.17	1.44	N.S.
Conditions x subjects ..	12	46	3.83	1.32	N.S.
Categories x subjects ..	16	125	7.81	2.71	<0.01
Residual .. ..	48	138	2.88		
Total .. ..	99	1,182			



to a real difference between two groups of conditions, equals and control on the one hand and 2 in. and 4 in. on the other.

## Experiment II

The second experiment was designed to check that the shift in P.S.E. was dependent on the inspection periods and not merely an effect of successive contrast.

Procedure. There was no initial inspection period and the periods between judgments were shortened from 10 to 5 sec. A second group of five subjects was used. In view of the level of discrimination of the subjects in Experiment I, it was decided to shorten the stimulus category intervals to 1 1/2 in. In view of the results of Experiment I, the control condition was omitted and the 4 in. inspection pattern was replaced by a 1 in. condition. Otherwise the design was identical with that of Experiment I. The analysis shown in Table 6 is again of totals of forward responses.

Results. The results of Experiment II are set out in Table 6. The mean difference between the equals and 2 in. condition yields  $t = 3.7$ , which for 32 degrees of freedom has  $p > 0.0001$ . Hence the significant main effect of conditions is due to a real difference between the equals condition on the one hand and the 1 in. and 2 in. conditions on the other.

The shift of P.S.E. between the equals condition and the disparity conditions is considerably smaller than in Experiment I (see Fig. 13). Subtracting the mean P.S.E. in the equals condition from that in the 2 in. condition gives an effect of 3.13 in. in Experiment I, and 1.04 in. in Experiment II. In terms of frequencies of forward responses the difference between the equals condition means in the two experiments is not significant

TABLE 6

## RESULTS FROM EXPERIMENT II

	Conditions		
	Equals	1 in. forward	2 in. forward
Mean number of forward responses ..	28.8	21.6	21.4
$\sigma$ m. .. .. .	1.88	1.36	1.96
P.S.E. .. .. .	0.5	0.59	0.54
$\sigma$ m.d.n. .. .. .	0.26	0.13	0.32

TABLE 7

## ANALYSIS OF THE VARIANCE OF THE FORWARD RESPONSES FROM EXPERIMENT II

Source	d.f.	Sums of squares	Estimated variance	F	p
Conditions .. .. .	2	35	17.5	9.35	<0.001
Stimulus categories .. .. .	4	945	236	126	<0.001
Subjects .. .. .	4	30	7.5	4.01	<0.05
Conditions x categories .. .. .	8	29	3.6	1.92	N.S.
Conditions x subjects .. .. .	8	8	1	0.53	N.S.
Categories x subjects .. .. .	16	32	2	1.06	N.S.
Residual .. .. .	32	60	1.87		
Total .. .. .	74	1,139			

whereas the difference between the 2 in. means gives  $t = 4.09$ , which for 80 degrees of freedom has  $p < 0.0001$ .

### Discussion

Thus I conclude that when the variable edge of the inspection pattern is closer to the subject than the standard edge, there occurs a shift in the P.S.E. towards the subject, i.e. variable edges of test figures appear farther away. There is no evidence that the size of this effect depends on the degree of separation of the inspected edges, 1, 2 and 4 in. being equally effective. But the process has been shown to be time dependent, since the addition of an initial 2 min. inspection period together with a doubling of the inter-judgment inspection period produced a significant increase in the size of the effect.

The results will now be considered in relation to the four hypotheses which the experiment was designed to test.

Hypotheses A and B: Stereoscopic fatigue and inversion. According to these hypotheses, the variance in the control condition, when the stimulus edges were not present in the inspection period, should be lower than the variance in the other conditions. The standard errors of the means in Table 4 reveal that the opposite of this prediction is true. The hypotheses are therefore contraindicated. These hypotheses could not account for the shift in the P.S.E. which occurred in the disparity conditions.

It may therefore be concluded that no pronounced stereoscopic fatigue or inversion was present in the experiments.

There is a possibility that fatigue, or the tendency to inversion, affects only the test stimulus which corresponds to the inspection stimulus.

If this were true, the response variability for those test stimuli would be greater than in the control condition. The results reveal no such tendency and therefore the presence of localized fatigue is not indicated.

Hypothesis C: Normalization to equidistance. From the analysis, the mean difference of forward responses between the control and both the 2 in. and the 4 in. conditions was significant, that is, there occurred a significant shift of the P.S.E. in a direction towards the inspection figure. Figures 12 and 13 show the psychometric functions from which it can be seen that the change in the number of forward responses was in the same direction for each of the stimulus categories. This implies a shift of the whole subjective scale of relative distance in the same direction.

These results strongly support the hypothesis that there is an adaptation to the "norm" of equidistance, and that this process is formally analogous to those normalization processes described by Gibson and Radner.

Hypothesis D: Three-dimensional figural after-effect. There is no strong evidence that variable edges suffer an apparent displacement away from the position of inspected edges as would be predicted from Köhler and Emery's satiation theory. But such effects may be masked by the tendency of scales to remain all of a piece with reference to the P.S.E., even when the latter undergoes a shift. There is, however, an indication of such a figural after-effect in data from Experiment I, shown in Figure 12. The equals conditions produced disproportionately large and small numbers of "forward" responses to the +2 in. and -2 in.

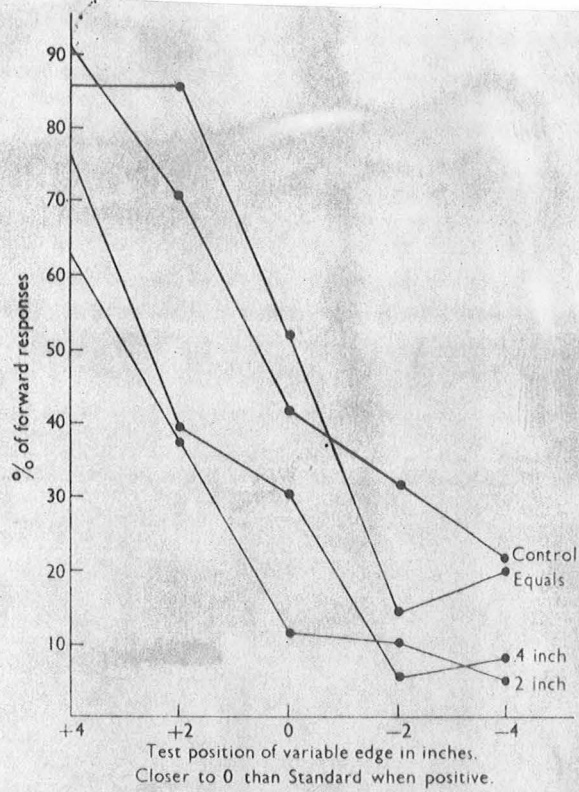


FIGURE 12

Psychometric functions for the four conditions of Experiment I.

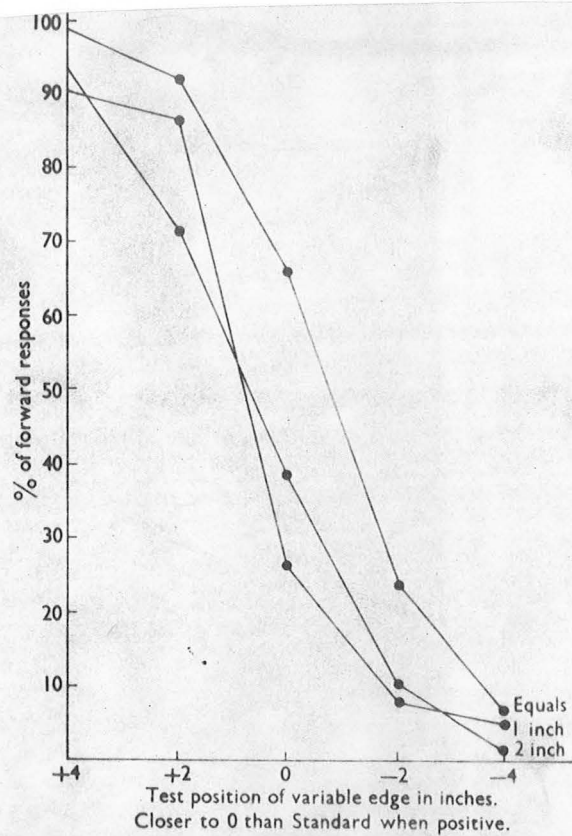


FIGURE 13

Psychometric functions for the three conditions of Experiment II.

test stimuli respectively. These are the test stimuli adjacent to the position of the inspection figure. However, this discrepancy was not sufficiently large to give a significant interaction between conditions and categories.

Similarly, the variations in the slope of the curves for Experiment II (Fig. 13) though not significant, are in the expected direction. The category interval 3 in. to 1.5 in. includes the position of the 2 in. inspection figure and the 2 in. curve is the steepest of the three. The interval 1.5 in. to zero includes the position of the 1 in. inspection figure, and here the 1 in. curve is the steepest. There is no inspection figure contained in the interval zero to -1.5 in. but the equals curve, with inspection figure at zero, is the steepest.

The main result of the present experiments may thus be summarized in two statements: (1) there is a tendency for non-equidistant objects to appear equidistant; (2) this tendency outlives the presence of the inspection stimulus and reveals itself as a shift in the whole scale of relative distance, in subsequently exposed test stimuli.

Statement 1 is confirmed in the work of others.

Werner (1938) exposed the two patterns of Figure 14a in a stereoscope. The frame did not appear to slant much in depth despite the considerable disparity of the half-images. He assumed that the primary correspondence was altered. As a consequence, the two equal length lines  $c_1 - d_1$  and  $c_2 - d_2$  were judged according to the new correspondence, and appeared to slant in the opposite direction to the frame. This so-called binocular depth contrast could be thought of as the simultaneous counterpart of the successive adaptation effect reported here.

Werner reported a similar effect with the stereograms shown in Figure 14b; there, two sets of lines were fused and the disparities in the lines  $a_1$ ,  $b_1$  and  $a_2$ ,  $b_2$  were said to induce a contrast tilting of the lines  $c_1$  and  $c_2$ .

Ogle (1946) attempted to explain this last effect in terms of cyclofusional eye movements which he said would be induced by the disparity of the outer lines. These cyclofusional movements would, he claimed, restore the correspondence between the outer lines and consequently introduce a disparity between the inner ones. This type of explanation is only possible for contrast effects produced by slant about a horizontal axis. In our experiments the relative depth changes are equivalent to a slant about a vertical axis and neither eye torsion nor other types of eye movement could "cancel" the retinal disparity.

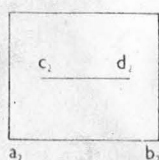
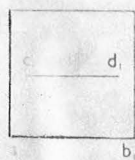
Gogel (1956) demonstrated an "equidistance tendency." This is a tendency for all parts of an object and for different objects to be seen in the same frontal-parallel plane when depth cues are weak.

Harker (1962), in a study of the role of cyclotorsion in binocular contrast, concluded that there are, as well as cyclofusion, "perceptual factors" which determine the apparent displacement of objects to the frontal-parallel position. One of the perceptual factors he suggested is the equidistance tendency.

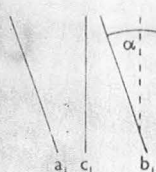
While all this evidence supports an interpretation of my results in terms of a central shift in the scale of binocular disparity, or in Werner's terms, a shift in stereoscopic correspondence, an explanation in terms of monocular factors cannot be ruled out.

In my experiment, the separation between the images of the standard





(a)



(b)

FIGURES 14a AND 14b

Patterns used by Werner to demonstrate binocular depth contrast.

and variable stimulus edges was constant in the right eye. We need only consider, therefore, the changes in the left eye. In the experiment the subject is shown a series of 50 random settings of the edges. The possibility exists that during this test series he builds up a subjective scale of monocular image separation of the edges. He could use such a scale as an indication of relative depth. In terms of adaptation theory, his neutral or equidistance point in this subjective scale would tend to centre about the mean of the stimulus series. In the control and equals condition this would correspond to objective equidistance, but in the 2 in. and 4 in. inspection conditions the inspection pattern would produce a retinal separation of the images of the edges in the right eye which would be to one side of the mean of the separations of the test series. A typical "anchor" situation would therefore result, and the shift in the subjective mean or equidistance point which would be expected could explain our results.

Monocular factors may also be invoked to explain Werner's depth contrast. The fact that the frame appeared to be more frontal-parallel than it should, may have been due to the suppression of one frame by binocular rivalry. Even if this were not the case, the narrower frame in Figure 14a may have caused the enclosed line  $c_1 - d_1$  to appear longer than the line  $c_2 - d_2$  in the broader frame. This length contrast would be induced prior to binocular fusion and would give rise to an apparent binocular disparity. The effect would not depend on the frame being seen in depth and would not therefore be a depth contrast effect.

In Figure 14b, the tendency to see as vertical, lines which are tilted away about a horizontal axis, which Ogle explained in terms of cyclofusion, could be due to a tendency for each tilted monocular image to normalize to the vertical.

Thus, although the tendency to see non-equidistant objects as equidistant seems to be well established as a phenomenon, it is by no means certain that a shift in the central stereoscopic disparity mechanism is involved.

SECTION 2ADAPTATION TO PRISMATIC DISTORTIONS

If the proximal optical array arising from an object is optically displaced or rotated the behaviour associated with it is appropriate to that same object in a position or orientation where it would normally produce that proximal optical array.

Many aspects of behaviour related to a visible object are affected by a disturbance of the normal position and orientation of the proximal stimulus with respect to the distal stimulus.

These behavioural disturbances may be classified into four main categories: (1) visual-motor co-ordination of movements other than eye and head movements; (2) the co-ordination of visuo-spatial judgments with eye and head movements; (3) behaviour related to mono-oriented objects; and (4) intersensory localizations. The first three of these disturbances will be discussed in the next three chapters.

## CHAPTER 4

### VISUAL-MOTOR ADAPTATION

Introduction. The most obvious consequence of wearing displacing spectacles is the disturbance of visually guided behaviour, such as pointing. Movements towards objects will be directed towards that position in space whence the displaced optical array would normally emanate. If the pointing limb is in view, the person will correct his initial mistake and be able to guide it visually to the target. Therefore, in any experiment in which the effects of distorting spectacles are being studied, the subject must not be allowed to see the moving part of his own body, at least until he has completed the movement.

Human subjects, given time and knowledge of results are able to adapt their movements to simple visual displacements or rotations. There has apparently never been any disagreement about this fact since the experiments by Stratton in 1896.

Other mammals can apparently adapt their movements to some extent also. Foley (1940) found that monkeys adjust some of their movements after wearing an inverting lens for eight days and Bossom and Hamilton (1963) found that they could adapt to a  $13^{\circ}$  lateral visual displacement after two days. Cats have been shown to adapt to displaced vision (Bishop 1959). We shall discuss the case of sub-mammalian species later.

The effects of rotary distortions of vision will be considered first.  
Inversion and Reversal of the Optical Array and Visual-Motor Co-ordination.

Stratton (1897) wore a lens system in front of one eye which inverted and reversed the optical array. He wore this device continuously for seven

days and gave a full account of his visual motor disturbance during that time. On the first day he reported that, "Almost all movements performed under the direct guidance of sight were laborious and embarrassed..... The wrong hand was constantly used to seize anything that lay to one side..... Relief was sometimes sought by shutting out of consideration the actual visual data, and by depending solely on tactual or motor perception..... In order to write my notes, the formation of the letter and words had to be left to automatic muscular sequence, using sight only as a guide to the general position and direction on my paper." (p. 344). By the third day he reported that, "I could watch my hands as I wrote, without hesitating or becoming embarrassed thereby..... Yet I often stretched out the wrong hand to grasp a visible object lying to one side; right and left were felt to be by far the most persistently troublesome relations when it came to translating visual into tactual or motor localizations" (p.349). On the fourth day he reported, "My hands, in washing, often moved to the soap or to the proper position in the basin, without premonition or any need of correcting the movement. At one time in the morning, I pictured the basin and its appurtenances before me in pre-experimental terms. But my actions were the opposite to those which would have been appropriate to this image." (p.352). He was still having difficulty with left-right visual-motor co-ordination. On the fifth day, however, he reported, "But I found that the appropriate hand often came to the appropriate side of the visual field directly and without the thought (frequently necessary before) that that visual side meant the other side in motor or older visual terms" (p.355). On that day

also he reported, "the most harmonious experiences were obtained during active operations on the scene before me. In rapid, complicated, yet practised movements, the harmony of the localization by sight and that by touch or motor perception - the actual identity of the positions reported in these various ways - came out with much greater force than when I sat down and passively observed the scene." (p.356).

Stratton gave himself no systematic tests of visual-motor co-ordination, he merely reported on those common actions which occurred in his normal routine of life. American investigators since Stratton have used experimentally controlled visual-motor tasks.

Ewart (1930) asked his three subjects to sort cards and to point to visual targets, before, during and after 3 one hour periods of inverted and reversed vision on 14 consecutive days. Snyder and Pronko (1952) timed the performance of a single subject at a card sorting task, the Minnesota Rate of Manipulation Test, the Purdue Pegboard, and a mirror-tracing task before during, and after the 30-day period during which inverting-reversing spectacles were continually worn. Both experimenters found that performance in the motor tasks steadily improved, provided there was knowledge of results. Performance was found to be disturbed for a while when the spectacles were removed. Snyder and Pronko used a control condition to investigate the effect of the constriction of the visual field which inverting spectacles necessarily impose. They found that this constriction of the field to  $20^{\circ}$  did not appreciably influence the quantitative or qualitative results.

Peterson and Peterson (1938) and Snyder and Pronko (1952) found that the visual-motor habits learned whilst wearing distorting spectacles were retained when the subjects were again tested with the spectacles

after a period of several months of normal viewing.

Erisman began working on the problem of displaced vision in 1928 at the University of Innsbruck. His assistant Köhler published a series of papers (1951, 1953, 1955, 1956a, 1956b, 1962) and has, since Erisman's death, been the director of the laboratory (see Kottenhoff, 1957a, 1957b for an English summary of this work). Köhler's approach is phenomenological relying on the introspective reports of his subjects, rather than on the application of controlled experimental tests. He used a variety of optical devices, inverting-reversing lenses, a mirror which inverted only, prisms which reversed left and right only, and displacing prisms.

He described various strategies which a subject may adopt in order to make movements to conform with inverted and reversed vision. Certain movements are not disturbed. A hand moving quickly to a particular unseen part of the body successfully reaches the target, even when the hand crosses the field of view, and thus appears to run in reversed fashion. The displaced vision is not impelling enough to disturb the automatic character of such movements. Writing may be done correctly and without difficulty if done as a set of learned, automatic, kinaesthetic-motor movements, with vision as only a guide to the general position of the paper. A subject writing in this fashion, with left-right visual distortion, reported that the movements of his fingers ran off automatically, as if controlled by some external agent. Every attempt to affect them intentionally led to complete blockage.

This procedure of kinaesthetic-motor guidance does not succeed when the task is to reach to, or follow, a visual target, for the visual



information is essential for the success of such tasks. Köhler distinguished between two types of task. The first is where the subject is required to initiate a rapidly executed reaching or aiming movement, such as kicking a ball, throwing a dart, or ordinary walking over rough ground. The second type of task is where the moving limb is in the field of view and may be guided continuously in relation to the visual target. The second type is not much disturbed by visual distortion.

For the difficult impulsive movements Köhler described various strategies. The first strategy which subjects adopt is to deliberately take the glasses into account and delay the motor response until the habitual movement may be inhibited and replaced by one which the subject predicts will hit the target. The method demands a fatiguing degree of concentration, and the reasoning is likely to fail when some unforeseen factor occurs which has been omitted from the calculation. When the situation is a potentially dangerous one, the subject becomes alarmed and all attempts to move in the direction which reasoning has decided are blocked.

The next strategy is the command to do the opposite of the habitual movement - to move the opposite ('wrong') foot or hand in the opposite 'wrong' direction. Here the point is not to decide first where objects really are and act accordingly, but to merely do the opposite of the first impulse. Mistakes are common with this method and movements are slow.

As time goes on, inappropriate movements become negatively reinforced by undesired outcomes, such as unintended impacts with objects or failure

to hit targets. Gradually it becomes sufficient for such false hopes to be only partially carried out for a 'warning' to result and the movement to be inhibited. At this stage the need for deliberate thinking diminishes, and correct movements begin to be carried out automatically. Köhler reported that for him the apparently inverted field of view passed in front of him, like the pictures on a cinema screen. He did not take them seriously, he achieved a "liberation from the visual picture". Eventually complex movements, such as ski-ing, climbing, cycling, and driving were correctly and smoothly executed. However, each new task had to be learned piecemeal; success at one skill did not transfer to other skills.

Köhler insisted that his introspective method revealed the essential "inner experience" involved in what he called rehabilitation to visual distortion. He was critical of Ewart, Snyder and Pronko, and other American workers after Stratton for their 'one-sided behaviourism'.

The Americans may have elicited a narrow range of responses from their subjects, but this narrowness need not have stemmed from their behaviourism. We claim that all that is capable of becoming communal knowledge (scientific knowledge) may be derived from observing the behaviour of others. Köhler need not himself have been a subject to have gained the knowledge he has. Having been a subject probably helped him to formulate ideas, but the experience was in theory not essential. The facts or ideas which Köhler reported are only more 'inner' than any other facts of science in that they were derived from the verbal reports of his subjects. They are now "outer" because they have become communicated, and therefore communal, facts and ideas.

Köhler was perhaps only attacking that form of behaviourism in which verbal reports are not allowed as evidence. Köhler's whole approach is otherwise a brave attempt to analyse the changes underlying rehabilitation in terms of visual-motor habits (see in particular Köhler, 1956b). He wrote ".....the path to correct seeing ..... can only be understood against the background of a theory of habits and their interweaving". Again, "It's clear that the goal of the subjects is to learn in some manner how to make correct movements. It is rather interesting to see how this happens, and how, gradually and unnoticed, behaviour transforms itself into seeing", (quotations from a translation by Gleitman of Köhler's 1953 paper). Köhler used what we consider to be non-behaviouristic terminology but otherwise made what amounts to a behaviouristic analysis with concepts which, for the most part, can be operationally defined.

Recently J. G. Taylor (1962) working in Innsbruck and South Africa, has presented what he claimed to be a full behavioural account of the experiments on distorted vision. His theory uses a Hullian framework and a notation derived from set theory. He came to rely also on ideas derived from Ashby's theory of multistable systems (Ashby, 1957). In spite of Taylor's intention to give a behaviouristic account of this field of study, his language is often subjective; he talks as if his formulae describe "perceptions", "experiences", etc., rather than observable behaviour.

Papert, who collaborated with Taylor, wore left-right reversing spectacles each morning over an extended period. The prediction was that habits appropriate to the distortion would be built up but at the same time

normal habits would be retained by being practised in the afternoons. A series of visual-motor tasks was administered to the subject while he wore the distorting prisms. These included reaching by command to particular objects, moving a hand or foot which was touched, executing complex commands to place particular objects in particular places, walking round a chair, riding a cycle, etc. It was found that training on one particular task did not transfer to others. It was this specificity of learning which lead Taylor to talk of the visual-motor system as a complex, multistable system.

Rhule and Smith (1959a, 1959b) also stressed the specific nature of sensory-motor learning with inverted vision. Their studies are puzzling in several ways. The four groups of subjects were asked to write rows of a's, triangles, and dots under four conditions; normal vision and normal kinaesthetic feedback, normal vision with inverted kinaesthetic feedback, inverted vision with normal kinaesthetic feedback, and inverted vision with inverted kinaesthetic feedback. By "inverted kinaesthetic feedback" was meant upside-down writing movements. How anyone can write a row of dots, or even a triangle upside-down is not made clear. Nor is it clear why upside-down writing movements should be regarded as inverted kinaesthetic feedback, which properly would involve an anatomical reversal of the kinaesthetic nerves in relation to the motor supply and vision. All that is reversed in drawing something upside-down is the pattern of motor-movements normally associated with the particular shape. The letter 'a' was the only one of Rhule and Smith's shapes which is obviously associated with a particular orientation of movements.

Their only measures of performance were the time during which the pen was in contact with the paper (manipulation time) and the time it was not

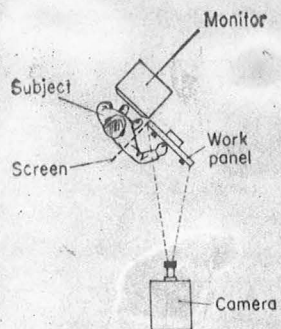
in contact with the paper (travel time). No measures were taken of the quality of the shapes produced. It is well known in mirror-drawing experiments, that time can be 'traded' against errors. A measure of either alone is no indication of the rate of learning. It can be seen from an illustration in Smith and Smith's book (1962, p.136) that the quality of performance was abysmal on the first day of the experiment. If the subjects were told to work as fast as possible, and we are not told what they were asked to do, their learning would not have been reflected at all in the time measures which were used.

Therefore there is no reason to trust any of the results which these authors present, and this applies to most of the results in the book by Smith and Smith, especially since many of their results contradict what we can find out from casual observation. For instance, they found that there was little if any difference in people's ability to draw 'a' and upside down 'a'. Anyone trying these two tasks is immediately aware that it is much more difficult to draw an upside down 'a', but one learns in a few minutes to become fairly proficient. The time-scale of averaged scores on each day for ten days which Rhule and Smith used, fails to display the learning which must take place here.

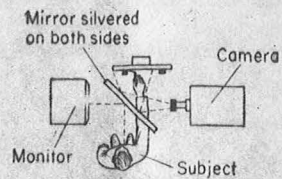
From the conditions where vision was inverted it was concluded that the effects of inversion were greater in tasks of increasing complexity. The triangle showed the most effect of inversion, the dots least. That the dots would show least effect should surely have been obvious before the experiment started, and to say that the triangle shows most effect, because it is the most complex shape, is meaningless in the absence of any independent measure of "complexity". Rhule and Smith concluded that learning was specific to each shape. Their

conclusion would carry more weight if they had tested whether training on one letter improved the ability to write other letters under similar distorting conditions. However, they did find that training to read upside-down writing did not transfer to writing with visual inversion (Rhule and Smith, 1959a), but in view of the crude measure they used, even this finding cannot be accepted as a fact.

These experiments and others by Smith and Smith which we shall presently describe were repeated using a closed-circuit television camera and monitor. The subject saw his hand and the visual target in the monitor only. The hand was actually off to one side where it could be photographed by the camera (see figure 15). The sideways displacement of the hand was a contamination. A better technique would have been to arrange the camera and monitor as shown in figure 16. In spite of their vast technical recourses, Smith and Smith apparently did not think of this simple device. Using the television system, Smith and Smith (1962 pp. 168-172) went on to analyse the relative disturbing effects, on drawing dots, a's, and triangles, of inverted, reversed, and inverted-reversed vision. Performance speed was most affected by inverted viewing, next by inverted-reversed viewing and least by reversed viewing. They concluded that this order reflects the order in which all skills are affected by these disturbances. This conclusion is completely unwarranted. Two of the shapes they used, dots and triangles ( ), are bilaterally symmetrical, so that reversal could not be expected to disrupt performance. It is not stated whether the order of drawing the rows of shapes was specified to the subjects, but in any case, inversion of the optical array would



**Figure 15** Arrangement used by Smith and Smith (1962) to study visual-motor disarrangement



**Figure 16** Suggested improved arrangement for studying visual-motor disarrangement

not disturb this aspect of performance, whereas reversal would.

Smith and Smith (pp. 180-183) also used a star-tracing task. This is the correct way to study the relative effects of the various types of distortion, for the figure is just as symmetrical one way as the other. They still found that inversion produced the greatest disturbance, and reversal least. They found, contrary to commonsense expectation, that movements in a particular dimension were not disturbed most by displacement in that dimension. For instance, those portions of the star figure which ran left to right were not most disturbed by left-right reversal of vision. This result is unacceptable for it is based on time measures only. Smith and Smith (1962, pp.185-210) also studied the effects of varying the position of the television camera in various planes relative to the hand executing given tasks. The tasks included assembly tasks, tapping a matrix of dots, drawing geometric shapes, writing, and maze tracing. For the details of these displacements and tasks, the reader is referred to the book by Smith and Smith. It was found that performance was not affected until the angular displacement of the seen hand reached about seven degrees, although the size of this "break-down angle" varied for the different tasks: the assembly task was most affected by a  $120^{\circ}$  horizontal displacement, other tasks were affected most by other degrees of displacement. Displacements in other planes than the horizontal and displacements of the panels upon which the movements were executed had differential effects for the various tasks and components of those tasks.

These studies do not lead to any important theoretical conclusions,



except that the effects of various types of distortion on various kinds of movement are highly specific, and one's faith in even this conclusion is shaken when one considers the crude measure used. Smith and Smith discuss their findings in terms of their neuro-geometric theory, which is discussed later.

In a recent paper, Smith and Greene (1963) report that children between nine and twelve years of age consistently failed to perform the drawing of dots, triangles and a's with inverted visual feedback. Children over twelve seldom failed to learn. But we are not told whether the younger children could write upside-down a's at all. If they could not, then it would be misleading to conclude that they cannot compensate for inverted vision in the case of this shape. My assumption is that learning to adapt to distorted vision involves a high level habit-substitution mechanism; it is reasonable to suppose that this mechanism will be relatively late in maturing. I would, like Smith and Green, predict that very young children are unable to compensate in the ordinary way for large optical distortions. Before I accept the critical age of twelve, I would like to see experiments done on children younger than nine and with a greater variety of tasks. I have found, for instance, that four-year-olds readily adapt their pointing, wearing 20 dioptre laterally displacing prisms. Anyone with a young child can verify my observation in a few minutes.

Visual-motor adaptation to disturbed visual input is most profitably studied using visual displacement, rather than inversion or reversal, for there is no contamination by the other disturbances which inversion and reversal entail. Furthermore, relearning is quicker

and therefore easier to study in a reasonable period of time, and also for this reason the experimental conditions are more easily controlled. The theoretically significant studies of visual-motor adaptation in recent years have involved the use of displacing prisms and mirrors.

The Site of the Recalibration Involved in Visual-Motor Adaptation.

Helmholtz (1962, Vol. 3 p.252) noticed how quickly pointing is adjusted to a displaced visual input. He argued from this observation that the visual-motor co-ordination is learned during the development of an animal. This is not a valid conclusion any more than would be the conclusion that visual-motor co-ordination is innate if it were the case that it could not be relearned by an adult.

Visual-motor adaptation involves a change in the control system which relates visual inputs to localizing motor responses. Harris (1963a, 1963b) has talked as if such a change were only one among the following possibilities: a change in visual perception; a re-orientation of the axes of perceptual space; motor response learning. But "visual perception" and "axes of perceptual space" are operationally definable only in terms of visual-motor behaviour. We fail to appreciate how all Harris's distinctions can be given operational significance. However, there are two apparently distinct possibilities.

These possibilities are that visual-motor adaptation may occur either on the afferent, or on the efferent side of the control system. Let us assume for the time being that this is a real distinction. There are no direct ways known for finding out on which side the change has occurred, but there are two indirect methods which might give some indication. The point of the first method is to discover

whether a subject, who has adapted his visual-motor behaviour to a displaced optical array, reports a target to be in a new position, or whether he reports his arm to be in a new position. In order to give such questions any meaning, one must define an independent criterion of directionality. In the course of a person's life time the verbal label 'straight ahead' has become conditioned to a particular position of eyes, head, image on the retina, and to a particular position of the pointing finger in relation to the body. The procedure consists in using these conditioned verbal responses to indicate whether changes have occurred in the afferent or in the efferent part of the total system which co-ordinates movements of the arm with the position of a visual target relative to the observer. The subject is alternately asked to set a light to the medium plane using vision alone and to point to the medium plane.

There would appear to be three main possible results.

(a) In the first place, a subject may come to attach the verbal label 'straight ahead' to a new position in space relative to his body. In other words he may recalibrate the visual input side of the visual-motor control loop in relation to this criterion. Any recalibration of the visual median plane may involve a recalibration, not of retinal space values, but of the position of the eyes in relation to a given position of the visual target. When I call this a recalibration of the visual median plane, I am using the word 'visual' to include the position of the eyes as well as the spatial position of images on the retinae. It is reasonable to conclude that any recalibration of the position of the eyes would

involve primarily the motor innervations to the eye muscles, rather than the kinaesthetic input from these muscles.

(b) The second possibility is that the subject will come to attach the verbal label 'straight ahead' to a new position of his arm. This could involve either the kinaesthetic inputs from the arm, or the motor innervations, or both. If the newly-labelled straight ahead position were displaced to the full extent of the experimentally produced displacement, it is reasonable to suppose that both kinaesthesia and motor innervation would have been relabelled. If the relabelling were limited to one system, the old labelling of the other system would conflict with the new labelling, and something less than a full change in the reported position of the arm would result. In either case, one would conclude that the visual-motor adaptation had involved a 're-calibration' of the motor-kinaesthetic output side of the visual-motor control loop.

(c) The third possibility is that the subject will relabel neither the visual median plane nor the kinaesthetic-motor median plane. After learning to hit the target, the subject will report that the light looks straight ahead but that he has to point to one side in order to touch it. One would conclude that he has not recalibrated any part of his visual-motor system. In ordinary language one would say that he has consciously made an allowance for the fact that the visual target, although appearing straight ahead, was in fact appreciably displaced to one side. This procedure and terminology appears to give us an operational behavioural definition of the term 'conscious adjustment'.

Although no details were given, Harris (1963b) apparently did an

experiment of this kind. When subjects were asked to point straight ahead (presumably in the dark), after having adapted their motor behaviour to displacing prisms, their pointing deviated in the direction of the visual displacement. Judgments of the visual straight ahead were not required, but Harris found that the auditory straight ahead was not affected. Our own experiment along these lines (Howard and Craske) produced results with such wide intra- and inter-individual differences that a clear-cut conclusion was impossible. The instructions, "set the unseen finger to straight ahead" and "set the light to the straight ahead" which were involved in the experiment, are essentially ambiguous. For instance, a light may be set either to the visual straight ahead, or to that position where it would be located if the hand were straight ahead. Part of the task of judging the visual straight ahead is knowing where the head and body are, and these are motor-kinaesthetic judgments which are also involved in the judgment of the motor straight ahead. I could find no way of overcoming this ambiguity. In other words, the judgment 'straight ahead' is perhaps not an independent criterion, and therefore cannot serve as an indicator of the site of recalibration.

The second procedure which could apparently serve to identify the site of recalibration is to investigate whether the effect transfers across hands and across eyes. Harris also argued that if the change involved in adaptation were visual, the subject would point in a similar way with either hand. However, he found that the learning did not transfer to the hand which had not been used in the training. Furthermore the adaptation with the trained hand was the same whether the target was a light or a sound. Hamilton (1964) confirmed that adaptation does not

transfer across hands; although he found a little transfer when the subject was allowed to move his head and body.

If the recalibration is of the proprioceptive-motor system, visual-motor adaptation learned with one eye open should transfer when tested with only the other eye open, Bossom and Hamilton (1963) have found that such transfer does occur in the monkey, and even in a monkey which has had both its corpus callosum and optic chiasma mid-line sectioned.

Helmholtz reported results which conflict with these recent findings; he found that adaptation to lateral displacement did transfer across hands but not across eyes. Whereas Harris concluded that the recalibration is on the kinaesthetic side, Helmholtz concluded that "...it is not the muscular feeling of the hand which is at fault or the judgment of its position, but the judgment of the direction of the gaze...." (Helmholtz, 1962, p.246). Harris concluded that, "when proprioception and vision provide conflicting information - when a person feels his hand in one place and sees it in another - proprioception gives way. The person comes to feel that his hand is where it looks as if it is."

Harris's conclusion does not follow from either his evidence, nor the other evidence cited. In the first place Harris failed to consider the change in motor outflow which is probably involved in visual-motor adaptation. We shall discuss this issue later. Our main criticism of Harris's conclusion is that it is based on the results of one type of training procedure. In this procedure, the subject was asked to point to a visual target. His first attempt was out by the amount of optical displacement and he gradually and deliberately altered

the direction of movement until he hit the target. His eyes did not have to modify their position, and the retinal image remained unaffected. Small wonder therefore that the recalibration affected the arm and not the eye. The subject had no option but to deliberately modify the position of his arm. Furthermore, it is not surprising that the effect of training transferred from one eye to the other, for there was no reason to suppose that anything had happened even to the eye which was open during training. In so far as the effect does not transfer from one arm to the other, one must assume that the visual-motor habits controlling one arm are distinct from those of the other. People constantly learn skills involving different movements for each arm, so that this specificity of habit recalibration is not surprising.

If a situation could be devised in which the eyes have to modify their movements in order to reach a target, then one might expect a visual recalibration and not a recalibration of a limb. I have devised such a task. The subject was asked to place the index finger of one hand in a straight ahead position. The lights were then put out and twelve-degree, laterally displacing prisms in spectacle frames were placed on the subject. He was asked to glance to one side keeping his head straight in the head clamp, and to return his eyes to his fingertip. The lights were then put on, revealing any errors to the subject. The lights were put out and the procedure repeated twenty times, the subject being asked to do all he could to succeed in having the correct fixation when the lights were put on. The learning transferred from one hand to the other. I could not test whether it transferred from one eye to the other, for the subjects could not dissociate their eye movements; the experiment ought to be repeated with one of those rare people who can do this. The

same experiment was repeated with sideways head movements with similar results.

Thus, considering the parts of the total control system involved in a particular visual-motor response, it seems that recalibration occurs only in that part of the system which the training procedure demands.

In a more recent publication, Harris (1964) has gone some way to meet these objections to his proprioceptive theory of visual-motor adaptation. He admitted that under certain circumstances it may be the felt position of the eyes in their sockets or of the head on the body which is affected by adaptation to a displaced visual array, and further admitted that the felt position of the eyes may depend on motor outflow rather than proprioceptive feedback. He has assembled an imposing array of evidence that his modified theory can explain visual-motor adaptation and even curvature after-effects. This latter effect he put down to a change in the felt direction of eye movements as the eyes scan a straight line after having inspected a curved line. His theory cannot, however, account for curvature after-effects produced with constant fixation, nor the occurrence of two opposed curvature after-effects at the same time (see page 4). Furthermore, there are other visual adaptation effects which cannot be explained in kinaesthetic-motor terms, for instance, the movement after-effect (especially two simultaneous opposed movement after effects), tilt adaptation, many geometrical illusions. Anomalous correspondence and monocular diplopia, and pseudo-fovea are further examples of displaced visual space values which it would be difficult to explain in every case in proprioceptive-motor terms. I do not suggest that these cases demonstrate that there has been a change in the anatomical



projections from retina to visual cortex but only that the visual information becomes coded in terms of a new visual spatial frame of reference. The crucial test is whether or not the new apparent field of view is recognized to be different to the old when both are simultaneously present. The case of binocular diplopia satisfies this condition ~~---~~ if the new space values were due to an altered sense of the position of the eyes, the new and the old impressions could not co-exist. Localized tilt adaptation and curvature adaptation are other cases of simultaneously present old and new space values.

I suggest that such simultaneous comparisons between new and old spatial judgments within a modality provide the only really adequate criterion for deciding in which part of the system the change has taken place. This criterion is not always available.

The criterion adapted by Harris and others is that of transfer of the new habits. The argument is that if the recalibration is limited to one component (.e.g an eye or an arm) in the control loop, when a component is replaced by the contralateral structure, the new calibration may or may not transfer, depending on whether or not that component is the one which has been recalibrated. But apart from the possibility of intramodal comparison which we have already mentioned, one cannot talk about localization in a single modality without reference to a motor act or some other modality; one probably cannot even find independent criteria (e.g. the median plane) to indicate the site of recalibration. Transfer experiments do not provide an adequate criterion for deciding what is meant by the locus of recalibration along the sensory-motor control loop; one may be able

to say only that the relationship between a particular input or set of inputs and a particular output or set of outputs has been changed.

The results of transfer experiments enable us to make this kind of identification : the identification of affected linkages, not of affected loci.

If the re-arrangement involved no more than the learning of "a new pattern of muscle contractions", Harris (1963) argued, then, when the subject uses an arm movement different from the one he practised with, the adaptation should be less than when he uses the well-practised movement. He found that when the arm movement was modified by asking the subject to point at other targets, the adaptation was at least as great as when they pointed at the practised target. Adaptation is apparently not limited to particular sensory-muscular linkages, although it presumably could be so limited if appropriate training were given. Freedman, Rekosh, and Hall (1963) also found transfer, though not always full transfer, when the movement used in testing differed from that used in training.

I shall not discuss the neurological theories of which centres are involved in visual-motor spatial co-ordination. These matters have been discussed by von Bonin (1950), Penfield (1954), Paillard (1960), and Myers, Sperry, and McCurdy (1962).

Smith and Smith (1962) describe what they call a neurogeometric theory. They stress the innate, specific nature of the muscular-neurological organization underlying spatially co-ordinated behaviour. The main points of this 'theory', as far as spatial behaviour is concerned, may be summarized by quoting from their book (pp. 126-127). "The spatial organization of motion depends on the ability of the

living system to react to differences in stimulation between specific points. These might be two points on the same receptor surface, two points located on two different receptors, or one point associated with an effector and another associated with a receptor. To carry out this function, the internuncial neurons of the central nervous system are associated at their dendrite endings with two specific points, and react only when a difference in neural activity exists between these two points. Thus the basic mode of action of internuncial neurons is that of differential detection instead of simple conduction.

"Motion is multidimensional; it is made up of three primary movement components - posture, transport, and manipulation - which are integrated into complex motion patterns. These components are differentially controlled at different levels of the nervous system, ~~and~~ in relation to different types of stimuli. Posture is regulated by gravitational stimulation; transport movements, by differences in stimulation between the two sides of the body; and manipulative movements, by the properties of hard space (objects, surfaces). In addition, motion integration demands that each component be regulated relative to the other components.

"The neurogeometric detectors of the brain are the heritable anatomical units which account for genetically determined behaviour."

It is not clear to what differences between stimulated points neurogeometric internuncial neurons respond. Do they code the distance between the points or do they record differences in the frequency, intensity, etc. of the neural activities at these points?

Neurogeometric theory seems to lack any identifiable features

of its own. It is a collection of statements stressing certain aspects of behaviour and stressing the need to look at specific patterns of neuro-muscular activity in behaviour. This approach is claimed by Smith and Smith to be superior to "the general inadequacy of animal-based learning theory when we attempt to apply it to human behaviour organisation" (p. 126). I would agree that the specific aspects of human neuromuscular organisation need to be studied, particularly when there is an applied problem, such as it met with in time and motion study (Barnes, 1949). But detailed, particularized studies of this kind cannot lead to important theoretical generalizations. The only generalization to emerge from Smith and Smith's book is that human skills are highly specific with respect to the variables they studied. But the mechanisms of general theoretical interest about animal movements are common to many animals species. Sherrington's experiments on the reflex organisation of the spinal cord, von Holst's on re-afference; Granit's on the fibre system; Magnus's on the labyrinthine reflexes; all these experiments could have been done on any mammal and they all made important contributions to our basic knowledge of motor co-ordination in man.

#### The Conditions for Visual-Motor Adaptation.

The first person to have studied the conditions for visual-motor adaptation to prismatic displacement seems to have been Wooster in 1933.

She studied the effects of wearing prisms which displaced the optical array 21 degrees to the right. In the various experiments, 72 subjects were tested. Each subject was tested while wearing the prisms for a short period on each of ten days or for as long as was

required to overcome the effects of the distortion, if less than ten days.

The subjects had to make rapid movements of the right arm towards the position of one of several small round discs. Normally, the arm and hand were hidden from view. In one condition it was not possible to touch the target and no knowledge of results was provided, at least not deliberately. In other conditions information regarding the true position of the disc was potentially available to the subject in one of several forms. The disc emitted a sound in one condition. In another, the subject was allowed to move his finger about until it touched the disc. In a third condition the tip of the finger could be seen when the localizing response had been made. Finally, the tip of the other index finger was used as the target, and the subject was allowed to touch it if he made the correct localizing response.

After ten days of practice Wooster found that, even with no knowledge of results, accuracy had increased until the subject's mean deviation from true localization was 40.5 per cent less than the deviation on the first day. In spite of Wooster's efforts to eliminate knowledge of results, some information must have been reaching the subjects. Wooster herself suggested that there was "unconscious adaptation to the reaching movements to the new kinaesthetic stimuli from the eye muscles". Presumably what was meant was that the subject's body faced the true position of the visual target, while the eye was directed to its displaced position, and that gradually the subject came to behave as if he were looking straight ahead - an

after-effect of asymmetrical eye position on the apparent median plane. It is a pity that this factor was not controlled by making the displaced visual target symmetrical relative to the body median plane for some of the subjects. I shall discuss the significance of this part of Wooster's work later.

The sound of the disc buzzer was found not to contribute towards increased accuracy of pointing. When subjects were allowed to slide their finger along until they touched the disc or when they were allowed to see their finger, there was a rapid improvement in accuracy. However the most rapid improvement occurred when the visual target was the tip of the other index finger and the subject was allowed to touch it. In this last condition, we suggest that the subject could have performed correctly by disregarding visual information, because he could 'feel' the position of the target. The task would have been a purely kinaesthetic-motor one and as such would have involved no distortion of sensory input. It is no wonder that this condition appeared to give the largest adaptation. This interpretation could have been tested by investigating the after-effect of this training on pointing at visual targets other than the finger.

Although Wooster enquired into the nature of the conditions necessary for adaptation of visual-motor co-ordination with prismatic distortion, very few definite conclusions emerged from her work.

Stratton, Köhler, Wooster, and others have stressed the importance of active movements in the adaptation of movements to optical distortions. However, von Holst and Mittelstedt (1950)<sup>were</sup> the first to formulate a definite hypothesis. On the basis of his observations on insects and fish, in which he re-arranged the visual

input, he concluded that the important thing in visual-motor co-ordination is the relation of actively produced movements of the body or parts of the body to changes in the pattern of stimulation of the sense organs; which these movements produce. Such changes in sensory stimulation consequent upon self-produced movement he called "re-afference". Stimulation of the sense organs produced solely by changes in the external world were called "ex-afference". An animal capable of orientating itself must be capable of distinguishing between re-afferent and ex-afferent stimulation. It does this by making use of information from the neural centres which control the movements of parts of its body. The changes in the stimulation of the exteroceptors which a given pattern of muscular innervation would normally produce is 'allowed for' in processing the information from the exteroceptors. This idea has something in common with Helmholtz's theory of unconscious inference.

Held has recently applied this hypothesis to the case of visual-motor adaptation and reported experimental evidence which is claimed to support it. The schematized process which he proposes is shown in figure 17. It is similar to the one proposed by von Holst except for the addition of the "Correlation Storage". The skeletal muscle represents any motor system that can be seen by the subject. In Held's words, "...the re-afferent visual signal is compared (in the Comparator) with a signal selected from the Correlation Storage by the monitored efferent signal. The Correlation Storage acts as a kind of memory which retains traces of previous combinations of concurrent efferent and re-afferent signals. The currently monitored efferent signal is presumed to select the trace combination containing the identical

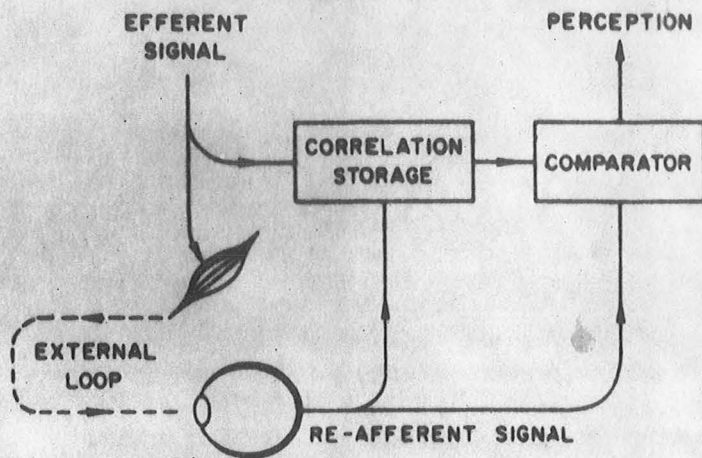


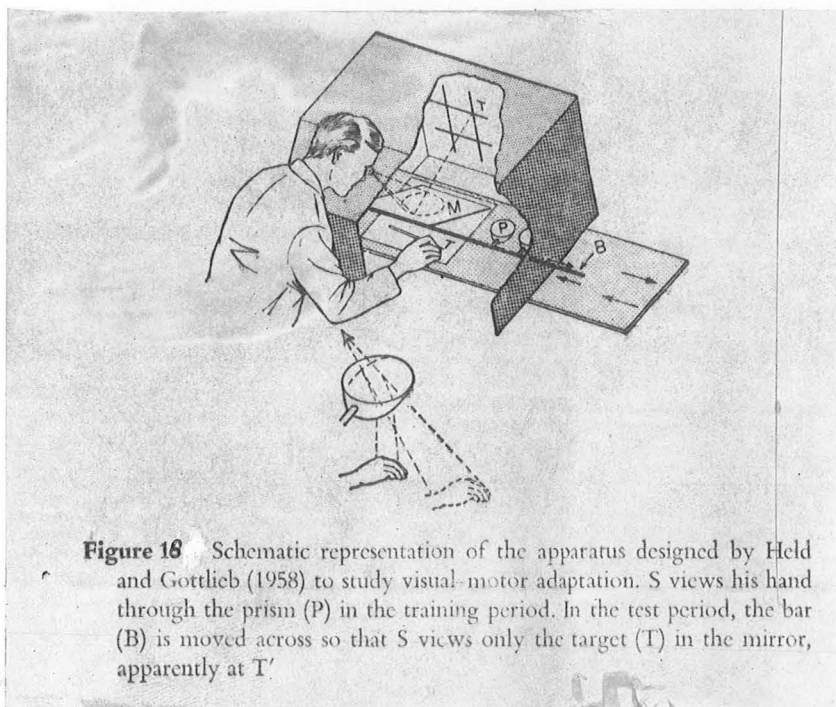
FIG. 17. Schematized process assumed by Held to underlie the consequences of rearrangement, neonatal development, disarrangement, and deprivation on visual-motor coordination.



efferent part and to activate the re-afferent trace combined with it. The resulting revised re-afferent signal is sent to the Comparator for comparison with the current re-afferent signal. The outcome of this comparison determines further performance." (Held, 1961, p. 30).

Held has been responsible for designing several very ingenious experiments. His experiments with neonatal kittens (Hein and Held, 1963) I consider to be some of the neatest experiments in the psychological literature.

Held's basic procedure was to compare the effectiveness of self-produced movement with that of passive movement in the re-adaptation of visual-motor co-ordination to a displaced visual input in adult human subjects. The experiments reported in Held and Hein (1958) and Held and Freedman (1963) are typical. They used an apparatus described by Held and Gottlieb (1958), which is shown in figure 18. This is similar to an apparatus described by Mowrer (1935). The mirror (M) or the Prism (P) could be moved into the subject's line of sight. The subject was first asked to mark the sheet under the mirror at the mirror-image positions of the four corners of a square. The subject was then allowed to see his hand through the prism for 3 min. while the hand was motionless, moved passively from side to side by the experimenter, or moved actively. Only the active movement condition led to any significant shift in the mean position of aim when the subject was again asked to point with the unseen hand at the corners of the reflected target figure. The active exposure had led to a change in the relationship between the visual location of the targets and the localizing movements made



**Figure 18** Schematic representation of the apparatus designed by Held and Gottlieb (1958) to study visual-motor adaptation. S views his hand through the prism (P) in the training period. In the test period, the bar (B) is moved across so that S views only the target (T) in the mirror, apparently at T'.

to touch them, and Held and Hein concluded that re-afference was necessary for such a change to take place. The failure of Weinstein, Sersen, and Weinstein (1964) to produce any adaptation even with an active condition was probably due to an experimental artifact as Held and Schlank (1964) pointed out. Weinstein et al. certainly produced adaptation with active training in their later studies, as we shall see.

I think that Held's conclusion that re-afference is necessary for visual motor adaptation to displaced vision is unwarranted. The reasons for my view will emerge in what follows. Held himself has acknowledged the strength of my arguments and has recently modified his extreme view.

#### The Role of Response Inhibition and Substitution in Visual-Motor Adaptation.

Anyone who tries to adjust his pointing to a displaced visual target will report that during the first few tries he has to actively inhibit his normal movement to the target, and deliberately make allowance for his error. When at last he 'gets the feel' of the correct movement, he has to practise it for a while before he is able to relax his active inhibition for the old habit. After a while the new habit becomes established firmly enough for him to report that he is responding 'naturally' to the position of the target. The after-effect produced when the prisms are removed surprises the subject. This demonstrates that, although the original recalibration was achieved only by deliberate inhibition and redirection, the new response, once established, acquires the status of an automatic habit. If it had to be maintained by a deliberate redirection of movement, the whole

subject of visual-motor adaptation would be trivial. It is only this final automatic stage which we refer to as visual-motor adaptation.

I suggest that where there is rapid adaptation of movements to distorted vision, over distances far greater than the normal range of error of those movements, an initial stage of gross inhibition of old habits and substitution of new responses must occur. I shall refer to this stage as response substitution, and we suggest that it involves activity at a higher level in the neuraxis than the level at which practised habits operate. A person can be told of the extent of an optical distortion before he makes any movements at all, and as a result he may hit the displaced visual target on the first occasion. Clearly then, the initial response substitution can occur no matter how the subject is informed of the distortion, and it is therefore meaningless to enquire into the necessary stimulus-response conditions for response substitution. Of course the information must be correct and the subject must be able to use it and be appropriately instructed. Enquiries about the necessary stimulus-response conditions for visual-motor adaptation must be concerned, not with the essential initial response substitution stage, but rather with the subsequent stage in which the new response becomes automatic. If optimum adaptation is required, an opportunity and a demand for response substitution should be given.

Held and Hein should have optimized the conditions for response substitution in their experiments. They did not do this and even in their active condition adaptation was only one third of the optical distortion. It is my experience that under different conditions of

training, full adaptation occurs after about ten active hits at the target with knowledge of results. Held and Hein's training consisted of merely inspecting the actively moved arm. With no visual target in view, the subject was not called on to correct any error, he was therefore not called on to make a deliberate effort to recalibrate his movements. Wertheimer and Arena (1959) were at a loss to understand why they were able to get fuller adaptation in a much shorter time than Held and Hein. But Wertheimer and Arena's training procedure involved placing crosses in visible squares. Their subjects were required to deliberately correct their movements. No wonder they got more rapid adaptation than Held and Hein. But even Wertheimer and Arena's procedure did not produce full adaptation, and that was because they allowed their subjects to guide their hands visually to the target; they were not forced to recalibrate their visual-motor habits.

Held and Mikaelian (1964) attempted to answer the criticism that in an unpublished wheel-chair experiment the passive subject was not motivated to make the effort necessary for adaptation. In the new experiment, all subjects wore  $11^{\circ}$  laterally displacing prisms. The active subjects were allowed to walk in a corridor, the 'passive' subjects propelled themselves in a wheel-chair. Only the 'active' subjects showed any evidence of a shift in their settings of a line to the median plane. There are several puzzling features about this experiment. Both groups of subjects were really active, what the experiment seems to show then is that re-afference associated with 'normal' movements is necessary for adaptation. But even this conclusion is not valid, for we are not told about the

precise nature of the passive subjects' experience. Were they allowed to see their bodies and the chair? If they were, they could visually guide the chair in relation to the seen sides of the corridor, and visual-motor adaptation would not be called for in order for them to succeed in avoiding collisions. Were they, on the other hand, prevented from seeing the chair or their bodies? If they were, they would not get visual feedback at the time and place of impact between chair and wall, and one of the essential conditions for adaptation would be absent. What is needed in these experiments, is that the part of the body which the subject is moving be hidden from view until after he has made his aiming movement, and that he then be allowed to see his error. The wheel-chair situation is much too cumbersome for controlling the information sequence which the subject is allowed to receive.

Weinstein, Sersen, Fisher, and Weisinger (1964) repeated Held's earlier wheel-chair experiment, in a corridor, rather than outside. They got the same amount of adaptation in the passive condition as in the active condition. One would like to know what information the passive subjects had to enable them to even know they had prisms on, let alone adapt to them. Were they able to see their own apparently asymmetrically placed bodies? In any case they must have had a field of view which was asymmetrical with respect to the body median plane, and this alone could explain the adaptation which would then have little bearing on the problems which Held was studying.

Held and Hein did not explore ways of presenting ex-afferent information. In fact, in some of their experiments, it seems that no ex-afferent information was available at all. The experiment of Held and Hein (1963) on neonatal kittens is another case.

In these experiments, an active moving kitten was linked mechanically to a restrained passive kitten (see figure 19). They both had the same visual experience of moving stripes, but the active kitten could relate the visual inputs to its own self-produced movements. This was the only visual experience either kitten had. Only the active kitten developed the ability to avoid a visual cliff, blink to an approaching object and extend its paws to a surface.

They showed in another experiment (unpublished) that this difference between the two animals could not be due to the effects of physical restraint on the passive animal. In this experiment, each animal was in turn active and passive, but when active only one eye was open, and when passive the other eye was open. It was now found that the animals could perform on the three tests only when their 'active eye' was open (or both). This result is surprising in view of all the evidence that interocular transfer of visual-motor habits occurs unless both corpus callosum and optic chiasma are sectioned (Downer, 1958). Presumably the ability to transfer skills itself depends on learning or maturation.

Held and Hein concluded that re-afferent stimulation is essential for the development of visual-motor co-ordination. I suggest that the passive kitten or 'passive eye' was never given usable ex-afferent stimulation. All it saw was a moving display of stripes. There were no other features of its environment to which it could relate this visual input. Held and Hein never tried to teach it anything. But there ~~is~~ a vast range of possibilities for correlated intersensory inputs which could be tried. For instance a visible object could be placed in the path of the animal; on some occasions the object could collide with the animal, and on other occasions the object could miss.



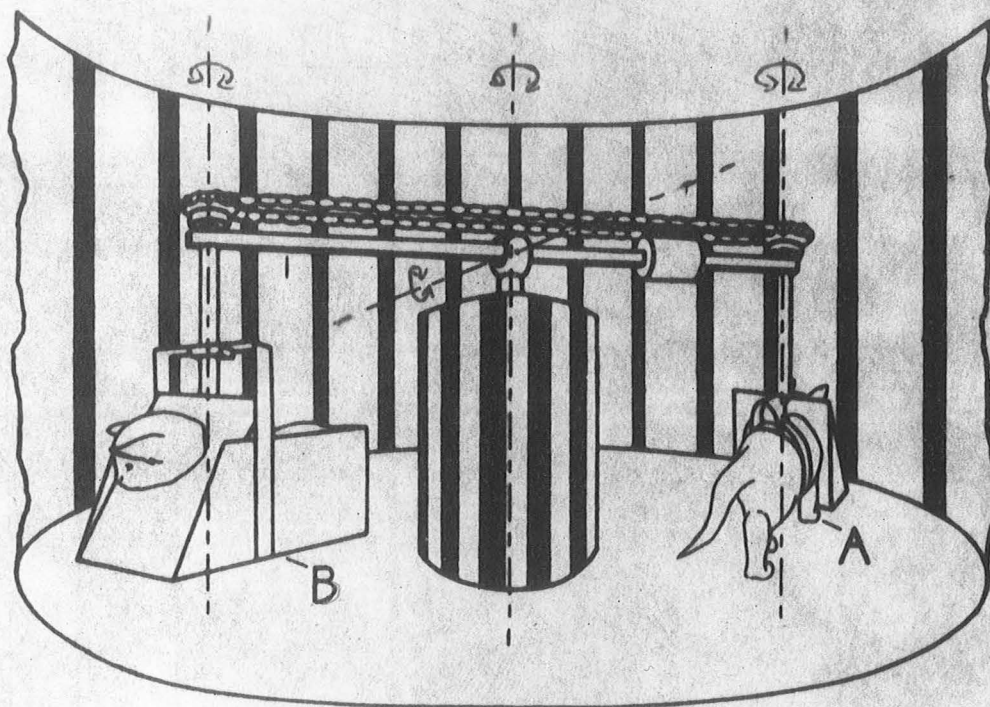


FIG. 19. Apparatus used by Held and Hein for equating motion and consequent visual feedback for an actively moving animal (A) and a passively moving animal (B).



To provide reinforcement (another thing Held and Hein failed to supply to the passive animal), the object could be food and sometimes hit the kitten in the mouth, or it could give an electric shock, or make a noise, pleasant or unpleasant. Another possibility would be to cause the passive animal to bump down a ~~visual~~ cliff and thus receive strong vestibular and tactile stimulation. In all this, one would merely have to ensure that the kitten could not move actively in such a way as to alter the visual signals. Eating movements, startle responses and the like would be permitted, for these would not affect the critical spatial feedback.

In view of all this, the surprising thing is the adequate performance of the active kitten on the tests. A possible explanation may be found in the work of Hubel and Wiesel (1963) and Wiesel and Hubel (1963a, 1963b) who showed that the visual receptor units which respond selectively to the direction and movement of stimuli are functional at birth but degenerate in a kitten which has been kept in the dark. Perhaps the experience that Held's active kittens were allowed to have was sufficient to prevent degeneration of these units, whereas the experience of the passive kittens was insufficient even though their visual experience was identical. If this were the case, experiments would need to be done to find out whether richer, purely ex-afferent stimulation would allow cortical units to develop normally. In any case, Held's evidence does not prove that the blink response, paw-placing reaction, and the visual-cliff response depend on learning, for there may have been retrogressive development in the passive kittens.

Apparently a newly learned adaptation to an optical displacement

is not stable when it has developed. Hamilton and Bossom (1964) found that subjects lose the prism after-effect, not only when they can view their own movements, as one would expect, but also when they sit quietly in the dark. Neither re-afference nor ex-afference are necessary for the re-establishment of the old habits. This is presumably due to the vastly greater strength of the old habits relative to the new.

I suggest that the effectiveness of self-produced, error-guided movements in bringing about adaptation is due to the demand and opportunity for response substitution which they provide. If passive movements were accompanied by a demand and opportunity for response substitution, then they too, I suggest, would lead to adaptation. But this is what has not been done by Held and his co-workers. The subject in such an experiment must be repeatedly asked to judge the position of his passively moved, hidden, arm in relation to a displaced visual target, and he must be given knowledge of results. If this is done, I make the following predictions. A subject trained to make estimates of his passively moved arm in relation to a displaced visual target will acquire a set of new judgments of the position of his passively moved arm in relation to the target. Secondly, I predict that his active pointing will be displaced significantly towards the real position of the visual target. In other words, new habits of passive pointing transfer, to some extent at least, to active pointing, just as new active pointing habits transfer to passive pointing. This is the crux of the question which Held and others have raised regarding active and passive training.

In order to test these predictions, I designed the experiment described in chapter 5.

Components of Kinaesthetic and Motor Activity in Visual-Motor Adaptation.

. There are four types of afferent and efferent activity associated with muscular contraction ~~identified~~; motor-outflow, activity of the muscle-spindle stretch receptors with their efferents, activity of Golgi tendon-tension receptors, and activity of skin and joint receptors.

The question is which, if any, of these four fundamental components is necessary or sufficient for visual-motor adaptation. It has already been shown that visual-motor adaptation can occur when none of these systems has been active during training, so that none of them is essential for adaptation. I have already enquired whether a recalibration of the judged position of a passively moved arm is sufficient; in this case it is presumably the joint receptors which are predominantly involved.

One may also ask whether any of the other possible combinations of the four efferent-afferent systems is sufficient to produce visual-motor adaptation, assuming of course, that the subject has optimum instructions and knowledge of results.

The various combinations are set out in table 8 with brief descriptions of the techniques involved, of the known capabilities of each combination, and of the known presence or absence of visual-motor adaptation in each case. The muscle-spindle system and the Golgi tendon receptors are grouped together; it is not easy to separate them in practice. No account is taken of skin receptors, on the assumption that the skin is anaesthetized throughout.

TABLE 8... Procedures for obtaining various combinations of efferent-afferent conditions of muscular activity, and their behavioural properties.

Receptors active	Procedures	Known and predicted capabilities	Visual-Motor adaptation
1. None	No movement	-	Occurs if discordant exafferent information is present
2. Motor-outflow alone	Self-produced movement with anaesthesia of all afferents	Accurate sense of amplitude of self-produced movement possible if loading is normal (Lashley 1917)	<u>TC DO</u> predicted with no load transfer
3a Spindle-Golgi receptors alone in passive movement	Passive movement of tongue or eye or anaesthetized joint	No position nor amplitude of passive-movement sense (Ludvigh 1953; Merton 1964)	<u>TC DO</u> not predicted
3b Ditto in active (not self-produced) movement	Stimulation of motor neurons with anaesthetized joint	No position nor amplitude of movement sense	<u>TC DO</u> <u>TC DO</u>
4. Joint receptors alone	Passive movement with severed tendons	Position and passive movement sense predicted	<u>TC DO</u> predicted
5. Motor-outflow and spindle-Golgi receptors	Self-produced movement of tongue or eye, or ischaemic paralysis of a joint	No position sense, but sense of amplitude of self-produced movement is possible if loading is normal (Merton 1964)	<u>TC DO</u> predicted with no load transfer
6. Motor-outflow and joint receptors	Self-produced movement with paralysis of spindle-Golgi afferents		<u>TC DO</u> <u>TC DO</u> predicted with load transfer if load change is not too
7. Spindle-Golgi receptors and joint receptors	No known procedure. Passive movement may be an approximation	Position sense and sense of amplitude of passive movement predicted	<u>TC DO</u> <u>TC DO</u> predicted
8. All three	Normal self-produced movement	Full capabilities	Present

Of these combinations, only 1, 7, and 8 have been studied in relation to visual-motor adaptation. One of Held and Hein's training procedures was to have the subject inspect his passively moved arm. They compared this training procedure with one in which the subject inspected his actively moved arm. It is not clear which systems are inactive in such a passive condition, compared with the active one. If the subject really relaxed, motor-outflow would be inactive, and Held and Hein seem to have assumed that this is the only difference between the two conditions. However, although the joint receptors are probably active in a similar way in the two conditions, the activity of the muscle-spindle system and Golgi-receptors is certainly different in the two conditions. These two systems will be active to some extent in passive movement but not to the same extent as in active movement. But it is unlikely that muscle-spindles and Golgi organs have anything to do with position or movement sensitivity; so the crucial difference between the two conditions, as far as the four factors are concerned, is probably the presence or absence of motor-outflow, as Held and Hein presumably believed. Even so, the fact that Held and Hein got adaptation only with active training could have been due to the way active movement tended to make the subject ~~to~~ attend to the discrepancy between the seen and felt positions of his arm.

Held (1963a) went some way towards meeting this objection. He compared the amount of visual-motor adaptation to a 20 dioptre prism, with self-produced movement and with the subject ineffectively straining against a swivel which forced his arm in an arc. Only the normal, self-produced movement produced any significant change in pointing. In the other condition, the visual feedback was said to

have been "de-correlated" from the motor-outflow. Held concluded that the effectiveness of normal self-produced movement is not due to any exertion of effort which "somehow potentiates the system". This does not really answer my objection, for de-correlated motor outflow may act as a distraction, inducing the subject to ignore his kinaesthetic inputs.

Although such passive training as Held and Hein applied did not affect pointing in an active test condition, this may have been because any 'recalibration' of the kinaesthetic system which such passive training may have produced was 'swamped' in the active test conditions by the old calibration of the motor-outflow. The proper test for any recalibration of the kinaesthetic system is to ask the subject to judge the position of his passively moved arm in relation to a visual target.

It can be seen from the table that I predict at least some adaptation when motor outflow and/or joint receptors are active, assuming the other conditions are optimized. This is because both these systems have been found to signal amplitude of movement. The muscle-spindle system is not thought to add anything to the ability to judge either position or amplitude of movement, its function not being sensory at all in the usual sense. It is unlikely, therefore, that muscle-spindle activity can either improve or reduce visual-motor adaptation under ordinary circumstances. A probable consequence of the absence of the spindle system would be that judgments based on motor-outflow alone would be easily disturbed by changes in the mechanical properties of the muscle tissue; for the spindle system is probably concerned with compensating for such changes.

The predictions in the table also involve statements about load transfer. I refer here to whether or not adaptation, trained when the limb is loaded to one extent, transfers to a test situation in which the loading is different. There is a continuum of loading values; where the limb has to pull against a resistance that it cannot move, where only its own internal friction is present, where its own friction is just overcome by a pull in the direction of movement, and finally where the arm has to pull back against a force in the direction of movement.

A change of loading will obviously affect the motor outflow, and in the absence of joint receptors (case 2) I predict that position sense will be distorted accordingly. Therefore transfer will probably not occur from one load to another when only motor-outflow is present, or when only motor-outflow and spindle-Golgi receptors are present.

When motor-outflow and joint receptors are active together, there should be some defence against distortions of position sense caused by load changes, and hence some transfer of adaptation from one load condition to another. The presence or absence of load transfer in these circumstances will indicate which of the two systems is most involved in visual-motor adaptation. If full transfer occurs it would indicate that the joint receptors are primarily involved. If no transfer occurs, it would indicate that the motor-outflow is primarily involved. This complex of problems has hardly begun to be investigated.

CHAPTER 5

An Experiment to Demonstrate  
Passively Generated Adaptation to  
Prismatic Distortion

In the typical training situation used by Held and his co-workers in support of their contention that reafferent information is a prerequisite for adaptation to displaced vision, there was ~~also~~ a discrepancy between the visual and kinaesthetic information available to the subject. However, I suggest that the discrepancy was not very obvious to the subject. Furthermore, I suggest that Held's training procedure, in which the subject inspects his hand through a prism, is a 'weak' one. In this procedure the discrepancy is continuously displayed to the subject with no instructions to utilize it in any way. This training procedure may be called 'continuous display training with no task'. It is the weakest form of training. A stronger form of training is to allow continuous viewing of the moving limb and to instruct the subject to hit a target, a procedure which may be called 'continuous display training with task'. This is still a weak form of training in that the subject can visually guide his finger to the target and ignore the discrepant kinaesthetic-motor information. The strongest form of training is to give a task but to allow the subject to view his finger only at the termination of each pointing movement, a procedure which may be called 'terminal display training with task'. The aim of the present experiment, which was carried out with the help of W. B. Templeton and A. Lowman, is to explore whether 'strong' training under conditions which do not give rise to reafferent stimulation (changes in sensory



input consequent upon self-produced movement) produce some shift of active pointing to visual targets.

### Method

Throughout the experiment the subject stood at a table just below elbow height with his head clamped in a head-rest. The subject's right forearm was firmly secured in a horizontal cradle designed to keep the arm rigid from elbow to index fingertip. The cradle was pivoted in the horizontal plane about the vertical axis containing the subject's elbow. It could be rotated either by active movement of the subject's arm or by means of a motor. The angular position of the cradle could be read off a scale attached to the pivot bearing. The subject's arm and the cradle were normally concealed by a screen which could be withdrawn to permit the subject to view his finger-tip.

Throughout the experiment the subject wore rotating prisms which displaced the field of view  $13^{\circ}$  to his left. The visual targets were two vertical brass rods which could be individually raised into the subject's field of view or lowered out of sight. They were located  $27^{\circ}$  apart on the horizontal arc of a circle centred on the subject's elbow and with a radius somewhat longer than the subject's forearm. Their optical positions (taking account of the prisms) were at equal distances on either side of the median plane of the head. Due to the spatial separation of the head and elbow, the  $13^{\circ}$  optical displacement as measured from the head corresponded to a displacement of  $12.5^{\circ}$  for the right target (target A) and  $9.5^{\circ}$  for the left target (target B) as measured from the elbow.

The pre-test consisted of six active pointings to each target

without knowledge of results; the first two pointings to each target were disregarded. This was immediately followed by the training session, during which the subject was several times instructed to keep his arm "completely passive". Movement was by means of the motor, and the subject instructed the experimenter when he was satisfied that he was pointing at the visible target; the screen was withdrawn and the subject could see his fingertip in its true relationship to the target; his arm was then returned by a circuitous route to the starting position for the next trial. Although the subject was not permitted to move his finger while the light was on he was encouraged to make deliberate correction of his pointing error on subsequent trials. Training was continued to an arbitrary criterion of ten successive trials *on none of which the pointing deviated from the true position of the target.* in the direction of its optical position by more than the magnitude of the optical displacement. This criterion was in all cases reached by about the sixteenth trial. Finally the post-test consisted of four active pointings to each target under the same conditions as the pre-test, but with instructions to point "normally and naturally" without the deliberate adjustments characteristic of the training session.

In all three sessions, the two targets and four starting positions, two to the left and two to the right, were balanced and presented in random order.

Sixteen subjects were used, mainly undergraduate volunteers.

### Results

Tables 9 and 10 show the optical displacement of each target as measured from the elbow together with the mean difference in pointing positions between the pre-test and the post-test.

The overall difference between pre- and post-test pointings is  $3.6^{\circ}$

Table 9 Individual data from the experiment on the effects of passive training on visual-motor adaptation to prismatic displacement. (All readings in degrees).

Subject	Pre-test mean		Post-test mean		Difference	
	Target A	Target B	Target A	Target B	Target A	Target B
1	81.4	104.0	73.5	99.2	7.9	4.8
2	84.9	113.2	78.5	111.5	6.4	1.7
3	81.5	105.5	79.8	104.3	1.7	1.2
4	76.5	101.3	71.4	96.3	5.1	5.0
5	73.8	99.9	71.5	97.6	2.3	2.3
6	83.0	105.0	77.5	100.2	5.5	4.8
7	83.8	107.6	80.6	104.9	3.2	2.7
8	74.7	105.2	71.0	98.0	3.7	7.2
9	71.7	96.3	67.4	94.9	4.3	1.4
10	76.5	104.7	73.7	100.6	2.8	4.1
11	74.7	101.9	72.0	99.4	2.7	2.5
12	69.4	97.6	67.0	93.8	2.4	3.8
13	79.1	107.3	76.1	104.7	3.0	2.6
14	81.0	101.0	76.5	98.4	4.5	2.6
15	85.8	109.1	81.6	109.0	4.2	0.1
16	81.9	106.8	77.7	102.2	4.2	4.6
Means	78.75	104.0	74.75	100.8	4.0	3.2

Overall mean difference = 3.6

$\sigma^2$  = 1.9

$t$  (15df.) = 10.3

TABLE 10

Optical displacement, and mean pointing position at the end of training and in the post-test as deviations from pre-test pointing positions, and the ratio of pre-test - post-test difference to optical displacement.

Optical Displacement	12.5°	9.5°
Mean difference between pre- and post-test pointings	-4.0°	-3.2°
Adaptation ratio	.32	.34
Mean difference between pre-test and final training level	-8.6°	-8.5°

$\pm 0.4^\circ$  which is of course very significantly different from zero.

The observed adaptation is thus one third of the optical displacement. My belief is thus confirmed, that training procedures can produce substantial adaptation of active pointing behaviour without involving reafference, when they force the subject to use the information about the distortion in the system.

The interpretation of this result depends on two crucial assumptions, that the arm was really passive during training, and that the subject did not make deliberate corrections during the post-test. Only instruction was used to ensure passivity, as was also the case when Held and Hein (1958) failed to obtain adaptation. The only evidence we can advance about the subject's attitude during the post-test is that of verbal report together with the fact that post-test pointing positions were quite different from the last four pointings to each target in the training session (see Table 8). It is well known that asymmetrical stimulation can induce its own characteristic after-effects. In this experiment the visual stimulation was approximately symmetrical about the median plane and the expected shift in pointing from pre-test to post-test was away from the median plane i.e. in the direction opposite to that which would be expected of an adaptation of the pointing itself.

CHAPTER 6An Experiment to Demonstrate the Effects of DiscordantEx-Afferent Stimulation on Visual MotorAdaptation to Prismatic Displacement.

There is evidence that other forms of exafferent stimulation can lead to visual-motor adaptation to displaced vision. I have already described how Wooster obtained some adaptation of pointing to a displaced visual target under passive conditions, and it was probably the visual asymmetry of the displaced targets in relation to the body median plane which induced this passive adaptation. In addition, Bruell and Albee found that visual asymmetry of the field of view about the fixation point affects the judged position of the median plane. Held himself found that passive inspection of curved lines leads to a visual curvature after-effect. It is not known whether any of these factors affect active pointing behaviour, and Held has never denied that they may. It would be interesting to find out whether or not they do.

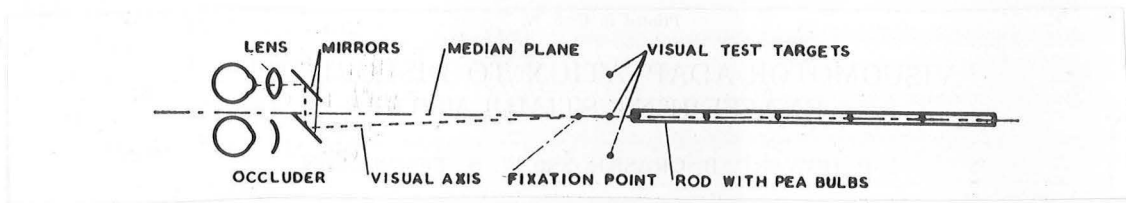
More recently Wallach, Kravitz, and Lindauer (1963) demonstrated that 10 minutes of inspecting the feet of one's own body seen through displacing prisms, led to some adaptation of pointing towards the real position of displaced visual targets. However, they did not run a control to reveal whether the effect of looking at the feet was due to the conflict of information from proprioceptive and visual inputs, or whether it was due to the visual asymmetry of the position of the feet relative to the body median plane. In the latter case, the effect would be the same as that reported by Wooster (~~see page~~). Craske and Howard repeated this experiment by having the subject inspect his feet through prisms when

his feet were physically off-centre by just the amount required for the prisms to restore them visually to the body median plane. No evidence of visual-motor adaptation was found, but the judgments of straight ahead which were used to reveal any adaptation effect were very erratic and a real shift may have been swamped. One would not expect much adaptation under these conditions, however; one's idea of where the feet are when one is relaxing is very poor, and therefore the discrepancy between the felt position and the seen position would not be evident.

The present experiment was designed to test whether prodding a person with a rod seen in a displaced position leads to visuo-motor adaptation. B. Craske helped in the administration of the experiment.

#### Method

Figure 20 shows the lay-out of the apparatus. The optical device consisted of two parallel mirrors which displaced the light from objects 2 inches to the left before it entered the left eye. Mirrors were used rather than prisms, because they do not introduce any apparent curvature, tilt, or colour fringes. The displacement is parallel rather than angular which is essential for our purpose; with prismatic <sup>g</sup> angular displacement the apparent displacement reduces to zero as the viewed object comes towards the subject. Mirrors have one disadvantage: they lengthen the optical path and hence reduce the apparent size (or increase the apparent distance) of the visual target. This means that where a series of visual targets is used, as in our experiment, the apparent distance between the targets is distorted and visuo-motor co-ordination will be disturbed accordingly. This disadvantage was overcome by introducing a lens system which magnified the displaced visual image to a size corresponding to its



**FIG. 20 Plan of the apparatus used to study discordant ex-afferent stimulation.**



distance.

The rod consisted of a rigid wood bar, the first 14 inches of which had five pea bulbs countersunk into the top surface at intervals of  $3\frac{1}{2}$  inches. The rod was mounted between rollers and could be moved towards the centre of the subject's lips. As seen through the mirrors, however, it appeared as if it would hit the face 2 inches to the left of the mouth. Nothing could be seen but the lights on the rod and a stationary fixation point. The lights used as visual targets in the test condition were three fine, one-inch-high light slits displayed 2 inches apart in the frontal plane at a distance of 17 inches from the subject. The centre light was in the subject's objective median plane and was therefore asymmetrical about the displaced visual axis.

The subject's head was clamped in a head-rest.

Each of the 20 subjects (10 male, 10 female) were subjected to two conditions.

In condition I, the subject was asked to look through the optical device and point to the target light. These appeared one at a time in random order, twenty times in all. The subject was allowed to fixate the slit displayed, and the hand could not be seen. This initial test established the pre-training deviation of the subject's pointing in relation to the displaced visual targets. He was then told to remain still and to fixate a light just above the rod, 12 inches away. The rod was then moved from a distance of 14 inches until it hit the subject on the lips. This was repeated 20 times. The subject was then immediately retested on the pointing task.

In condition II, the same procedure was employed except that in the training, the rod did not quite touch the subject. The order of conditions was alternated over subjects with an interval of at least a week between

conditions.

## Results

The results are set out in tables 11 and 12.

The 'being hit' procedure produced a significant mean change in pointing of  $0.64'' \pm 0.16''$  towards the actual position of the target lights, i.e. about  $1/3$  of the displacement. This difference is significant,  $t = 3.9$  which, for 19 d.f. has  $P = 0.001$ .

The 'not-being hit' condition produced no significant mean change in pointing. The size of the effect did not differ between sexes, nor between hands, though it tended to be larger for the right hand. Nor did the effect vary in size from the first to the last set of 10 judgments.

## Discussion

I have thus shown that discordant ex-afferent stimulation of an inactive observer leads to some adaptation of pointing towards displaced visual targets.

The effect could not have been due solely to the visual asymmetry in the position of the rod and the target lights, for this was present in the control condition, where no adaptation occurred. The tactile stimulation was symmetrical, so that there was no need to have a control condition where the subjects were touched without being able to see the rod. Apparently all active movement was prevented, even convergence of the eyes. Even more care was taken<sup>than</sup> by Held in his 'passive' conditions. I am forced to the conclusion therefore that discordant ex-afferent stimulation, which gives a passive subject 'information' regarding optical distortion, may lead to at least some visual-motor adaptation.

Table 11 Mean errors in arbitrary scale readings(1/120th.in.) for each subject from the experiment on discordant ex-afferent stimulation.

Subject	Condition I, rod touching		Condition II, rod not touching	
	Pre-test	Post-test	Pre-test	Post-test
Male	150	143	125	182
	177	-37	147	-42
	237	119	143	142
	852	864	695	576
	31	-148	161	164
	274	379	253	282
	104	88	158	194
	29	2	128	148
	327	306	128	146
	211	100	190	194
Female	377	220	191	226
	213	198	196	200
	210	176	87	169
	253	125	269	165
	199	202	202	214
	137	76	93	-17
	89	-119	201	227
	657	565	618	649
	423	386	456	430
	218	-11	302	266
Total mean error	258	181	232	226
Mean error in inches	2.15	1.51	1.94	1.88

An analysis of variance revealed that the only significant main effect is that due to conditions. A t-test was done on the effects of conditions with the data summed over all other factors, which gave  $t(19df.) = 3.9, p < 0.001$ .

TABLE 101

Mean error in inches of pointing at targets optically displaced  
2 in. laterally, before and after 'being touched' and 'not being  
touched'.

	Not being touched	Being touched
Before	1.94	2.15
After	1.83	1.51
Adaptation	0.06	0.64

In a recent paper Held and Mikaelian (1964) have modified the categorical assertion that re-afference is essential for visual-motor adaptation in conditions not involving intra-field distortions. They wrote, "The conditions which have so far been shown to produce adaptation to rearrangements without self-produced movement do not appear to have the generality shown by involvement of the motor-sensory feed-back loop. As far as is known, these conditions do not yield full and exact compensation for rearrangement.....". I have no quarrel with this statement; it does seem that passive training is not as effective as active training, and if this is Held's thesis, there is as yet no good evidence to refute it. Weinstein, Sersen, Weisinger, Fisher, and Richlin (1964) obtained 100% adaptation of active pointing after 10 minutes of passive inspection of the feet seen through  $7^{\circ}$  prisms. But I have already argued that this procedure produces an asymmetrical eye position which could be partly responsible for the reported effect.

The main issue is still to be settled by experiment; namely, are there conditions of passive training which are as effective as active training? Held by his phrase "As far as is known", clearly admits that there may be.

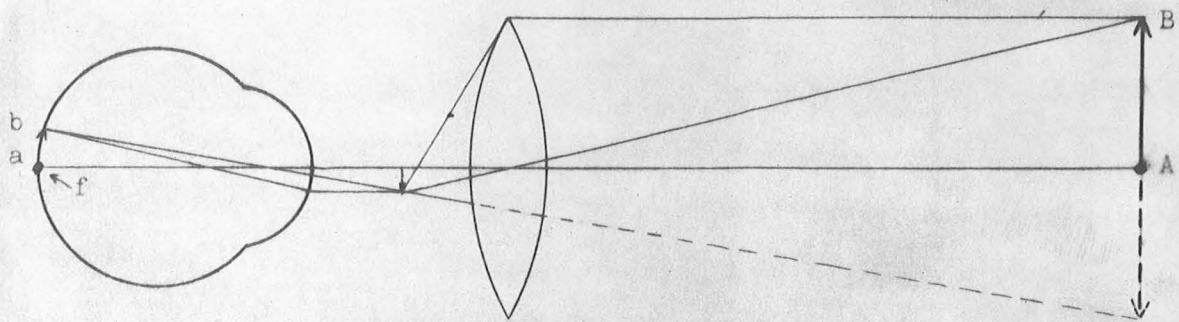
## CHAPTER 7

Adaptation to the Unusual Retinal Image MovementConsequent Upon Wearing Prisms BeforeThe Eyes

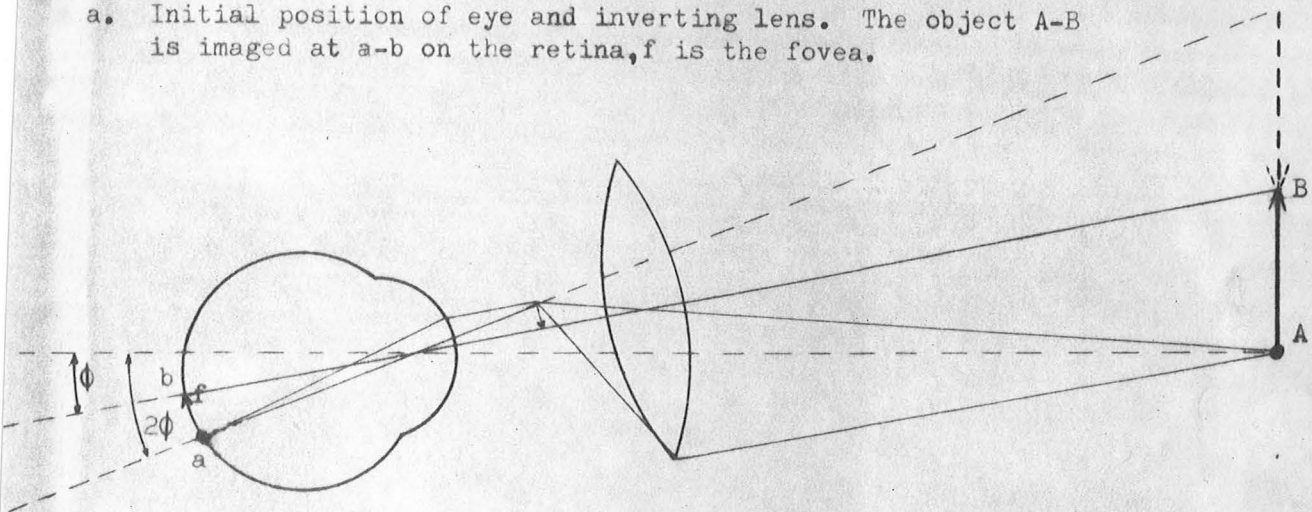
I must first consider the basic geometry of the relationship between movements of the eyes and head, and the resulting movements of the retinal image when inverting and/or reversing devices are worn. There are three cases to be considered. The lenses may be attached (a) to the subject's eyes, (b) to the subject's head, and (c) to a stationary object outside the subject. I shall assume for simplicity that the field of view is only inverted, that only one eye is open, and that the eye and head rotate about the centre of the eye's lens, from which all angular measures are taken.

The geometrical consequences of case (a) are shown in figure 21a and 21b. As the front of the eye is elevated through an angle  $\phi$ , the optical system moves through the same angle, carrying with it the visual axis. If A and B are two distal stimuli, and B is  $\phi^\circ$  above A, then under normal conditions the image A' is above image B' on the retina and a change in fixation from A to B by means of an upward eye movement (downward retinal movement) causes a corresponding upward movement through  $\phi^\circ$  of images A' and B' on the retina. If, however, inverting prisms are attached to the eye, image 'B' is above image A' on the retina. In this case a change of fixation from A to B is achieved by means of a similar upward eye movement (downward retinal movement). But bringing image B', which is above image A', to the

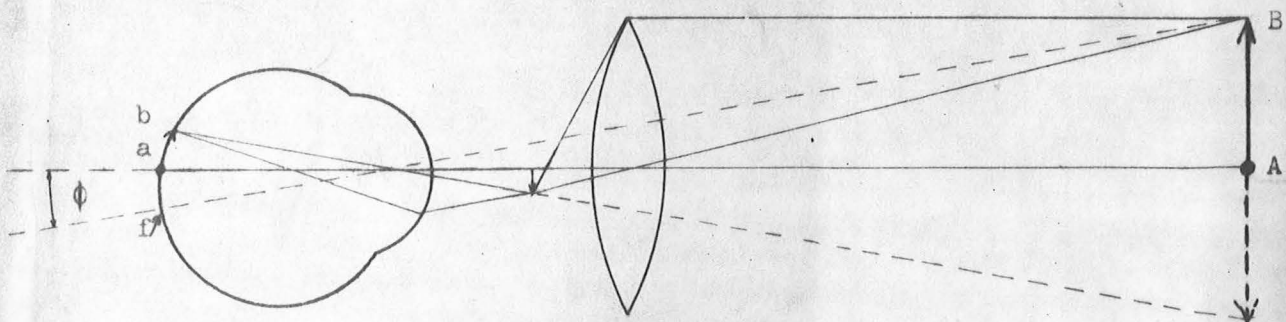
FIG. 21. Diagrammatic representation of the effects on retinal-image motion of wearing an inverting optical device.



- a. Initial position of eye and inverting lens. The object A-B is imaged at a-b on the retina, f is the fovea.



- b. The eye and inverting lens move together through angle  $\phi$  until the optic axis of the system is directed at B; the retinal image of the target moves through  $2\phi$  in the same direction as the eye, and the direction of gaze corresponds to the actual direction of the object imaged on the fovea.



- c. The eye moves through angle  $\phi$  while the lens remains stationary; the retinal image remains stationary relative to the target, and the direction of gaze does not correspond to the actual direction of the object imaged on the fovea.



centre of the retina in this way must involve a downward movement of the two images on the retina, i.e. relative to an outside standard the images move in the same direction as the retina and twice as far.

Movement of images on the retina through the same angle and in the opposite direction to movement of the retina itself (the normal case) signifies a stationary distal stimulus; stationary images on the retina signify a stimulus moving at the same speed and in the same direction as the eye movements; and movement of images in the same direction as the retina and twice as fast (the case when wearing inverting prisms), normally signifies a distal stimulus moving in the same direction and twice as fast as the eye movements.

If the subject's head is tilted backwards or forwards, the consequences are the same as for eye movements. When a subject, wearing inverting lenses on his eye, attempts to move his gaze from point A to point B, his normal habits, which determine the direction of eye movements relative to the position of the image of the visual target on the retina, will cause his eye to move in the wrong direction. He will move his eye down and his gaze will retreat away from the point which he was instructed to fixate. However, there will be one sense in which his old habits will be appropriate. If he is commanded to look at, for example, his feet, and if he ignores the inverted visual world, then past habit will indicate that a downward movement of the gaze is required, as indeed it is, even with the inverting devices on. In practice, however, the habits governed by the geometry of the retinal image dominate the meaning-mediated habits, for subjects on first wearing inverting devices built on contact lenses (Taylor, 1962, p.224)



have to learn to direct their eyes to specified points in space.

We have been assuming that the optical distortion is an inversion only. Movements of the eye to left or right will not be accompanied by an unusual movement of the retinal image. A left-right reversal of the optical array entails anomalous consequences for lateral movements of the eyes but not for vertical movements.

Both purely inverting and purely reversing devices introduce anomalous consequences if the eye is rotated about the visual axis. In practice, one must tilt the head and eye together. In this case, the retinal image rotates on the retina through the same angle that the eye describes, but in the same direction. Therefore the retinal image rotates twice as far as the eye relative to a fixed point in space. If the head rotates to one side through  $45^{\circ}$ , the subject will report that the field of view has rotated through  $90^{\circ}$ . The fixation point does not change of course, just as it does not change in normal vision in these circumstances.

Papert gave mathematical expression to these geometrical facts using complex number rotation (Taylor, 1962, p.189). The geometry of the situation is not so difficult to comprehend as Papert's treatment would seem to imply.

When devices which both reverse and invert the optical array are worn, there are anomalous consequences to both sideways and up-down movements of the eye. Rotations of the eye about the optic axis, however, do not now cause any anomalous rotation of the retinal image. This should be obvious when one considers that the distortion produced by any inverting-reversing device is radially symmetrical; a rotational shift of such a device relative to either subject or stimuli can

therefore have no consequences. This is clear when one thinks of an ordinary astronomical telescope.

To summarize the case where the optical device is worn on the eye; the relation between the direction of eye or head movements and the direction of the change of fixation in actual space is the same as in normal vision. But, the relation between eye or head movements and the direction of movement of the retinal image is the reverse of what it is in normal vision.

The geometrical consequences of case (b), where the device is attached to the subject's head, depend on whether the eye alone moves or the head and eye together. If they move together, the consequences are the same as case (a). If the eye alone is moved, the consequences are as shown in figure 21c.

As the line of sight is elevated the retina moves over an objectively stationary optical image in the opposite direction. This is just what happens in an eye under normal circumstances as far as the rays entering the eye are concerned. The subject receives the same proximal visual stimulation as he does when he scans a really inverted world without spectacles, that is, his retinal image moves in the usual way relative to the direction of his eye movements. However, the relation of the direction of his eye movements to the direction of the real objects in space is different to what it is with normal vision. When the eye is elevated, objects which are objectively lower than the initial point of gaze are brought into view. The situation is the reverse of case (a). The relation between the direction of eye movements and the direction of the change of fixation in actual space is the reverse of what it is in normal vision. But, the relation between eye movements and the movement of the retinal image is the

same as in normal vision.

In case (c) the optical device is attached to a stationary object outside the subject. The geometrical consequences of moving the eye or the head are the same as the consequences of moving the eye alone when the device is attached to the head. Table 12 summarizes this discussion.

I have avoided stressing the subject's judgments in this account; but have confined myself to the purely geometrical consequences of the various cases. What those judgments will be may be predicted for a naive observer, using Helmholtz's maxim, that "objects are always imagined as being present in the field of vision as would have to be there in order to produce the same impression of the nervous mechanism, the eyes being used under ordinary normal conditions." (Helmholtz, 1962, p.2).

The usual experimental procedure is to wear inverting devices fixed to the head (case 2 in table 13) and, in accordance with Helmholtz's maxim, the disturbed relationship between direction of eye movement and direction of retinal-image movement results in reports that head movements cause the field of view to move through twice the angle in the opposite direction.

Whether these judgments will change as the subject continues to wear the device will depend on the behavioural interactions between him and his environment. There is ample evidence that after several days of continuous wearing of inverting spectacles subjects report a stable scene when the head is moved. Stratton (1897) wrote on the third day of wearing inverting lenses, "Head-movements were still accompanied by a slight swinging of the scene, although in a markedly

	Relation between direction of movement and movement of retinal image.	Relation between direction of movement and direction of change of gaze in space
Devices worn on eye Eye or head movement	Retinal image moves through twice the angle in the same direction.	Normal relationship
Device worn on head Head movement Eye movement	As (a) Normal relationship	As (a) Line of gaze in space moves through equal and opposite angle.
Device fixed externally Eye or head moves	Normal relationship	As (bii)

TABLE 13. The Geometrical consequences of wearing  
inverting or reversing devices in  
various ways.

less degree than on the first day. The movement was referred more to the observer, so that it seemed to be more a moving survey of stationary objects." (p. 349). By the fourth day, "the swinging of the scene during movements of my body seemed greater or less, according to the way in which I represented to myself this movement of my body." (p. 354). By the sixth day, "Movements of the head or of the body, which shifted the field of view, seemed now to be in entire keeping with the visual changes thus produced; the motion seemed to be towards that side on which objects entered the visual field, and not towards the opposite side, as the pre-experimental representation of the movement would have required. And when, with closed eyes, I rocked in my chair, the merely represented changes in the visual field persisted with the same rhythmic variation of direction which they would have shown had I opened my eyes." (p. 358). Ewart (1930) also noticed the gradual increase in the apparent stability of the field of view as he moved his head after several days of wearing inverting spectacles.

Wundt (1894, p. 164) maintained that, "If the position of objects in space is inferred from movement, the retinal image must be inverted, since only where this is the case is it possible for the movement to correspond with the actual position of the objects. So far from being a paradox, the inverted retinal image is necessary for vision."

Coyle (1907), an undergraduate, pointed out the fallacy in this and similar arguments in the literature. We have already shown that, whether or not an optical system attached to the eye produces an erect or inverted image, it does not upset the normal relationship between the direction of eye movements and the direction of movement of the line of sight in space.

Stratton (1907) was convinced that his experiments disproved the eye movement theory of visual spatial localization. In those experiments, the lenses were attached to the head, so that the eyes had to move down to bring into central vision an object which was objectively above the initial fixation point. In spite of this inversion of the normal relationship, Stratton was able to achieve a new and adequate visual-motor co-ordination, which he claimed would have been impossible on an eye movement theory of localization. But Stratton has not disproved the eye movement theory, he has only shown that the signals from the eye movement centres do not have an immutable space value. Whether or not eye movements play an essential role in visual spatial localization is another question.

Recently Kottenhoff (1957b) has obtained quantitative data on adaptation to the anomalous motion of the visual image produced by right-left reversing spectacles. While wearing the spectacles a subject was rotated at a steady speed on a revolving chair placed inside patterned screening. He was asked to remember the apparent speed of the pattern and compare it with the speed of an actually moving pattern seen when rotation had stopped. Testing was apparently repeated at intervals over the three-hour period for which the spectacles were worn.

We are not told what the subjects did during these three hours; Kottenhoff's measure of the field motion would be contaminated by the visual after-effects of movement, and by nystagmus induced by the rotation, as well as by a time order error. He claimed to have demonstrated that only extraverted subjects show a decrease in the "field motion". His results could equally well have been due to his

two groups of subjects having differential habituation to the after-effects of rotation.

Taylor and Papert (1955) made much of the reduction of apparent motion in their discussion of the learning processes involved in adapting to inverted vision. They described how, with normal vision, there is a 'constancy' mechanism by which eye or head movements and the accompanying retinal-image movements are cancelled out to produce a stable judged field of view. When inverting spectacles are worn, a new set of equivalences must be built up between head movements and the movements of the retinal image. Apparently all subjects learn to stabilize their judgments, but some, according to Taylor and Papert, "also eventually report that the perceived world no longer appears to be inverted." It was predicted that those who continue to report an inverted world will, when they remove the spectacles, report an apparent rotation of the field of view at twice the angle in the opposite direction to tilts of the head. On the other hand, it was predicted that those who come to report an upright world will, after removing the spectacles, report a rotation of the field of view in the same direction as tilts of the head in the frontal plane. There is evidence to support Taylor and Papert's first hypothesis: Kohler (1951) reported that one of his subjects described the apparent movements of the field as opposite to the direction of head tilts. But Taylor and Papert could find no evidence in support of their second prediction. This is not surprising, for the prediction is based on a false analysis.

I have already argued that once a subject wearing inverting spectacles has learnt to move correctly and to stabilize the field of view, then his answer to the question "does the world appear erect?" is dependent

on higher-order skills associated with mono-oriented objects in the visual field. A change in his answer to this question will not affect his visual-motor co-ordination, nor the apparent stability of the field of view, during the time the spectacles are worn. This being so, there is no reason to expect that it will affect them after the spectacles are removed. Taylor and Papert appear to think that adaptation produces an actual change in the geometry of the situation, and that there is a causal connection between the reported orientation of objects and the reported movements of the field of view during head movements.

I have discussed this issue with Taylor, and while we understand each other's position, we have agreed to differ until there is more evidence.

To show that Taylor and Papert's second prediction is false, it is only necessary to consider what would happen in a world composed solely of polyoriented visible objects, such as cubes and spheres. Subjects would at no time report an experience of inversion; they would, however, have to learn to move correctly and to stabilize their judgments of movement, and no doubt, after removing the spectacles, they would experience the movement of the field in the opposite direction to their head movements. If mono-oriented objects were placed in the field of view after motor co-ordination and movement stability were completely adapted, these would be reported as being upside-down, and further learning would be necessary before they were reported as erect. But there is no reason to suppose that this learning would affect the already established skills.

Inverting optical devices may upset not only the normal relationship between eye movements and movements of the retinal image, but also that between optokinetic and vestibular nystagmus.



These two reflexes normally complement each other; but if left-right reversing devices are worn, the slow phase of optokinetic nystagmus will be in the opposite direction to the slow phase of vestibular nystagmus. Visually induced nystagmus will probably dominate the situation, so that there will still be compensation for retinal-image motion.

## CHAPTER 8

### Adaptation to Disturbed Visual Polarity

Ever since the seventeenth century when Kepler described the eye and revealed that the retinal image is inverted relative to the distal stimulus, scientists and philosophers have disputed how it is that the visible world is not reported to be upside-down. This history has been recounted many times and need not be repeated here. The reader is referred to Hyslop (1897), Walls (1951a), and Polyak (1958).

It was against the background of these philosophical disputes that Stratton (1897a, 1897b) conducted his famous experiments in which he wore lenses which inverted and reversed the retinal image so that it became objectively erect. According to Giannitripini (1958) the first experiment of this kind was conducted by Ardigo (1886) who reported that objects were eventually seen as upright, and that when the optical devices were removed, objects at first appeared upside-down.

The traditional question which these early studies attempted to answer was: does a person wearing inverting spectacles ever come to see the world right-way-up? This is a very ambiguous question and attempts to answer it have led to controversy and confusion. Before an attempt is made to analyse this issue, Stratton's reports while wearing inverting-reversing prisms will be briefly described.

On the fourth day of wearing his prisms Stratton wrote, "Objects in sight called up the ideas of neighbouring objects in

harmonious spatial relation with the things I saw ..... the movements of my legs and arms were, without my willing it, imaged in terms of the newer sight. ....the spatial reference of the touch perceptions was following with greater vividness the direction given by the new visualization. "Further on he reported ....during active movements of the body ..... the feeling of the uprightness of the scene was much more vivid than when the body was quiet." On the eighth day he wrote, "As long as the new localization of my body was vivid, the general experience was harmonious, and everthing was right side up. But when, for any of the reasons already given----- an involuntary lapse into the older memory-materials, or a wilful recall of these older forms-----the pre-experimental localization of my body was predominantly in mind, then as I looked out on the scene before me the scene was involuntarily taken as the standard of right direction, and my body was felt to be an inharmonious position with reference to the test. I seemed to be viewing the scene from an inverted body."

Stratton's reports were ambiguous, not because he gave an ambiguous answer to an unambiguous question, but because the question which his protocols are supposed to answer is an ambiguous one. Stratton was not to blame, the confusion is not in his reports, but in the people who have expected to find in those reports a clear answer to a misleading question.

In the years following Stratton's experiments some writers (e.g. Carr, 1935) concluded that Stratton came to experience an upright world, others (Woodworth, 1934; Higginson, 1937; Ewart, 1930, 1937) concluded that he did not. Peterson and Peterson (1938) and

Snyder and Pronko (1952) repeated Stratton's experiment but could not give a conclusive answer to the question. Snyder and Pronko's subject, when asked whether things looked upside-down, replied, "I wish you hadn't asked me. Things were all right until you popped the question at me. Now when I recall how they did look before I put on these lenses, I must answer that they do look upside-down now. But until the moment that you asked me I was absolutely unaware of it and hadn't given a thought to the question of whether things were right-side-up or upside-down." (p.113).

The question, 'does the world appear upright?' can mean at least three things. 1. It can refer to whether or not movements are effectively related to visual targets. We shall call this the motor-coordination upright. 2. It can refer to whether visual judgments of the direction of objects correspond to judgments based on other modalities. We shall call this the intersensory upright. Of particular significance here is the relation between vision and the gravity senses. 3. It can refer to behaviour associated with mono-oriented objects such as chairs, people, houses, etc. The visible world is polarized, that is, the sky, the ground, and most objects maintain a fairly constant orientation to gravity, to one another, and to the observer, under ordinary circumstances. There are situations, for instance when one is climbing a cliff face, where the polarity of the field of view is ambiguous, but even in such circumstances, visual polarity is unambiguously defined by the direction in which objects heavier than air can be seen to fall and substances lighter than air, such as smoke, can be seen to rise. Many things are polarized left-right

as well as up-down. For example, writing, traffic-flow, shoes. Left-right polarity is not geometrically analogous to up-down polarity, for one is defined with reference to the asymmetry of the human body and the other with reference to the centre of the earth. East-West- and North-South polarities are analogous to up-down polarity; compasses and sunsets are examples of such polarities.

I shall refer to the objective, geometrical orientation of the visible world in relation to the earth's centre, body asymmetries, etc., as the polarity of the visible world. If the polarity is the usual one, the distal stimuli are said to be upright, left-right correct, etc. Mono-oriented objects retain the same polarity with respect to each other, and this intrafield polarity can be appreciated by an observer even if his ability to detect the objective <sup>polarity</sup> of the whole field is absent.

People live in a consistent visible world most of the time, and consequently develop habits which enable them to behave adequately in such an environment, but inadequately when the polarity of the distal stimulus is altered. Left-right polarity can only be altered with reference to an observer, the up-down polarity of the visible world may be altered with reference to gravity and/or to the observer. Behaviour is therefore polarized, and we shall refer to the observable consequences as behavioural polarity, i.e. the tendency to behave towards mono-oriented objects in terms of earth- or body-based co-ordinates irrespective of the present orientation of the objects.

One consequence of behavioural polarity is the use of words, such as 'upright', 'inside- out', 'back-to-front', 'wrong-way-round', etc. But these words are often ambiguous, and are best avoided.

Simple discrimination tasks make the best behavioural indices of the polarity of behaviour, for they can be most precisely specified.

I suggest the following tests.

- (a) The speed of recognition of mono-oriented objects. A particularly good test of this kind is recognition of a person's face or identification of a facial expression as a smile or growl. A complex shape, such as a face, is particularly affected by changed orientation. The mouth of an erect smiling face is concave at the top like the mouth of an inverted growling face (see figure 22). The technique used by Rock (1956) of asking a subject to select a training shape from among several test shapes in various orientations is a useful one.
- (b) The correctness and speed of identification of the top and bottom of mono-oriented objects displayed in various orientations.
- (c) The speed of recognition that a falling object is falling, or that smoke rising - in other words, the ability to recognize 'polarized movements'.
- (d) The first figure to be recognized in a composite ambiguous figure in which the alternative figures are separated by a specified angle (see figure 23). Köhler (1953) used a Schröder staircase and asked the subjects which way they would approach it to climb the stairs.

It is not legitimate to use pointing or other directional movements to indicate behavioural polarity; for instance, if a subject were asked to indicate by pointing the direction in which he anticipates an object

FIG. 22

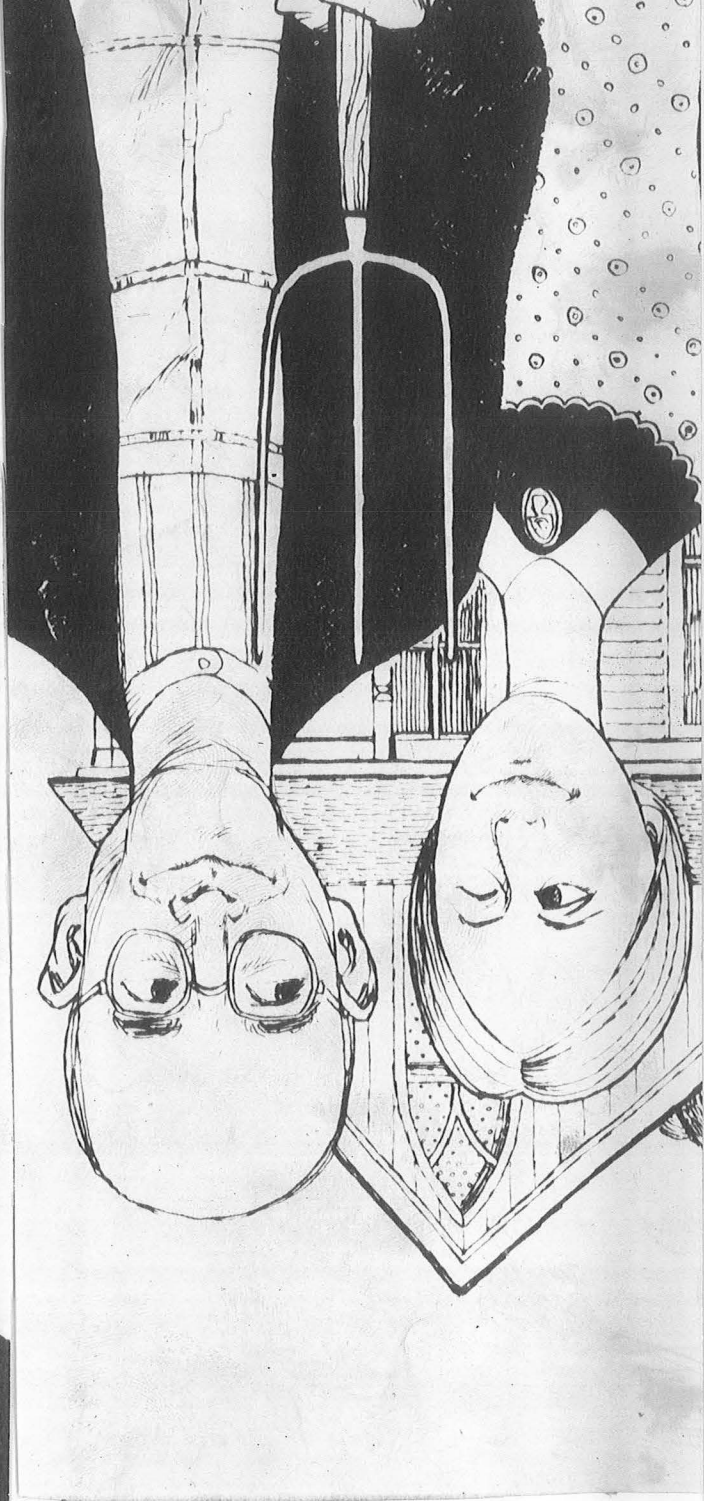
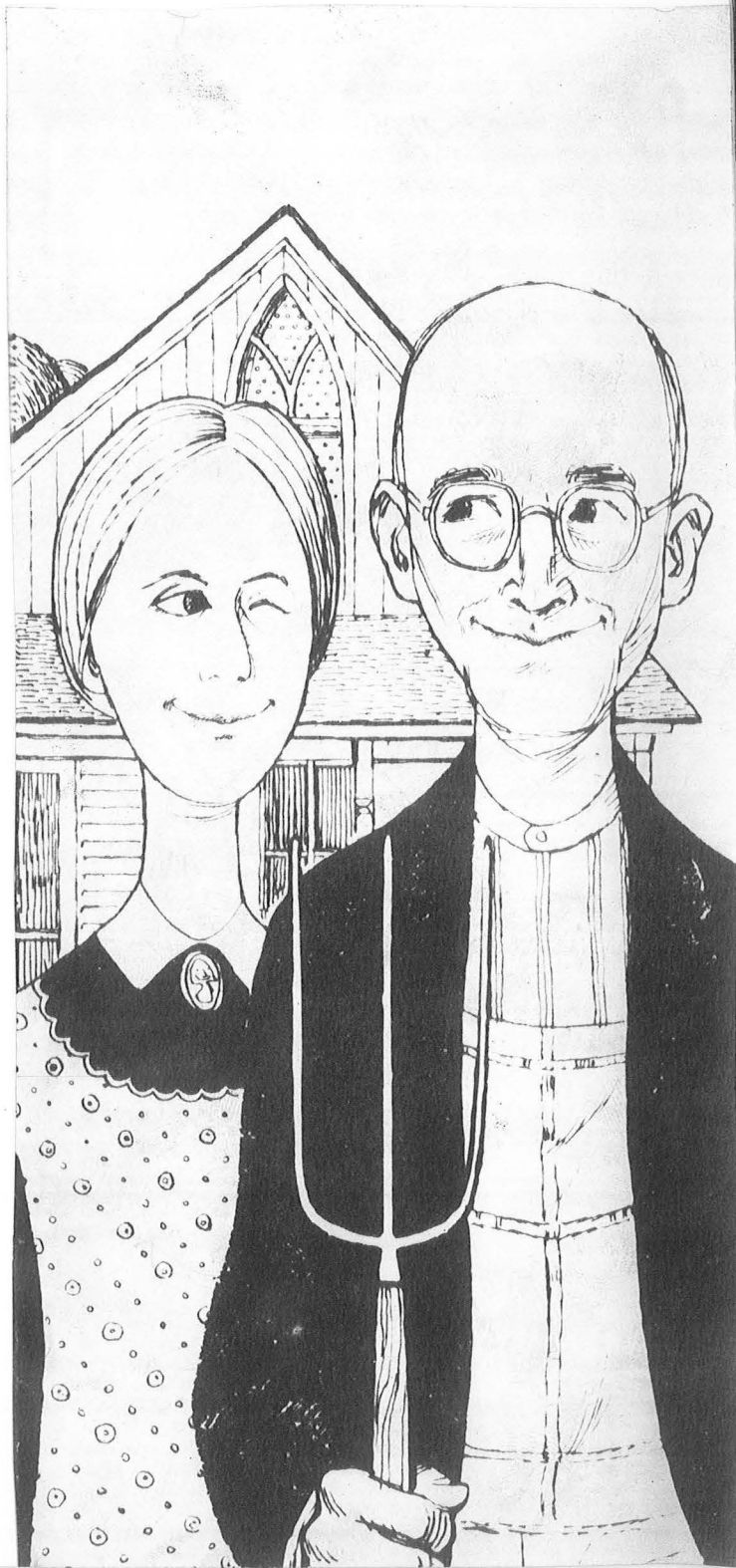






FIG. 23 Figure used by Thouless to study the effect of polarity on visual recognition.



will fall, he may do one of two things. In the first place he may point objectively downwards because this is his usual response, and, of course, he would be correct. This aspect of his old behavioural polarity will not be disturbed by the visual inversion and therefore it can give no clue to those polarized habits which are affected by the inversion. On the other hand, if the object which is going to fall is seen against the background of a room, he may anticipate that it will fall in the direction of the displaced floor of the room. In purely visual terms, he will be correct, but if he points in that direction, he will be pointing in the objectively wrong direction. All this response will indicate, is that the subject expects the object to fall to what he can see is the floor. In a purely visual sense, he will be right, but it is not what we want to know. What we want to know is whether the fall, when it occurs, is discriminated speedily and faultlessly as a 'fall' and not as a 'rise'. We can only get to know the answer to this question by eliciting discrimination responses such as correct verbal labelling, or some other equivalent, conditioned response.

I do not claim that these behavioural indices exhaust the definition of behavioural polarity, but they are sufficient to demonstrate that the concept is real and distinct from motor and intersensory co-ordination, and that discrimination responses are necessary for its measurement.

I thus have three broad operationally defined interpretations of the question, "does the world appear upside-down"? They are, the motor-co-ordination upright', the 'intersensory upright', and the 'behavioural-polarity upright'. Each one of these involves a

complex of habits, and each habit may be retrained independently.

Most writers have ignored the fact that there are these three aspects to the question of the visual upright and endless dispute had resulted (see for example Pickford, 1956).

I have already shown that people wearing inverting spectacles can adapt so that their 'motor-co-ordination upright' becomes correct. It also seems that their 'intersensory upright' adapts to the distortion. It remains to enquire whether their polarity behaviour can adapt.

Polarity is a purely visual matter, it has no necessary connection with other modalities nor with gravity. A world in which there was no gravity could still be polarized. A person with no gravity receptors other than vision could still appreciate that our world is polarized, and if he maintained a constant orientation of his body to his visual surroundings his behaviour would become polarized. Even if he did not maintain a constant orientation, he could still appreciate that mono-oriented objects remain in a constant relationship to one another, and he could still judge the direction of gravity in most visual surroundings, whatever he called it. If such a hypothetical person suddenly gained gravity receptors he would have to learn to relate the inputs from them with visual polarity. To see the direction in which things fall and hang is just as much gravity reception as interpreting signals from the otoliths. Both indicate the direction of the earth's centre. Visual signals mediate righting reflexes in man and in animals. Righting reflexes based on vision, known as dorsal light reactions, occur in many animal phyla; coelenterates, insects,

crustacea, and fish (Fraenkel and Gunn, 1961, Ch.10). They occur in such animals whether or not their other gravity receptors are functioning.

Vestibular signals also mediate unlearned righting reflexes in both men and animals, but in spite of having these reflexes, men must learn to judge 'up' and 'down' on the basis of vestibular signals just as they must for visual ones. But Erisman (Pickford, 1956), and Gibson and Mowrer (1938) claim that we can only judge the direction of gravity visually if vision has been associated with signals from other gravity receptors. We do not agree, for a 'purely visual' person can be taught to judge 'up' and 'down' in most natural environments. The fact that it would be easy to fool him is not significant, for it is also easy to fool a purely vestibular man, by putting cold water in his ear for instance or putting him in a centrifuge. In fact, in ordinary circumstances, visual judgments of the vertical, by a plumb line for instance, are much more accurate and reliable than judgments based on the so-called gravity receptors. In order to utilize visual polarity for motor responses, the position of the eye in the head and of the head on the body must be sensed, but vestibular stimuli are equally useless if the position of the head is not sensed. When Gibson and Mowrer wrote that "visual lines are not in their own right stimuli for orientation", they should have added that vestibular signals are not adequate in their own right either. Normal response mechanisms are needed in both cases, but verbal and motor discrimination based on each modality can be taught independently of the other.

Only mono-oriented objects can be said to be upside-down in a

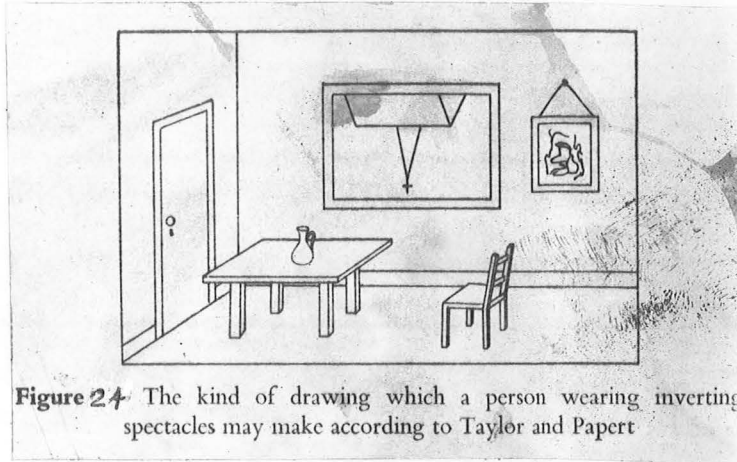
purely visual sense, where questions of motor and intersensory co-ordination are not considered. Therefore, inverting spectacles cause only mono-oriented objects (and movements) to be reported as being 'upside-down'.

The world is 'polarized', and if the righting reflexes are unlearned, this implies that the visual system itself is polarized with respect to certain features of the environment. Even so, we presumably learn to behave differentially to most of the polarized features of the world, and verbal responses such as 'up' and 'down' must be learned. This being so, it is reasonable to suppose that human beings can fully adapt most, if not all of their behaviour to inverting spectacles, so far as behaviour associated with visual polarity is concerned. Logically, of course, one cannot conclude that skills which were initially learned must be capable of drastic reorganization.

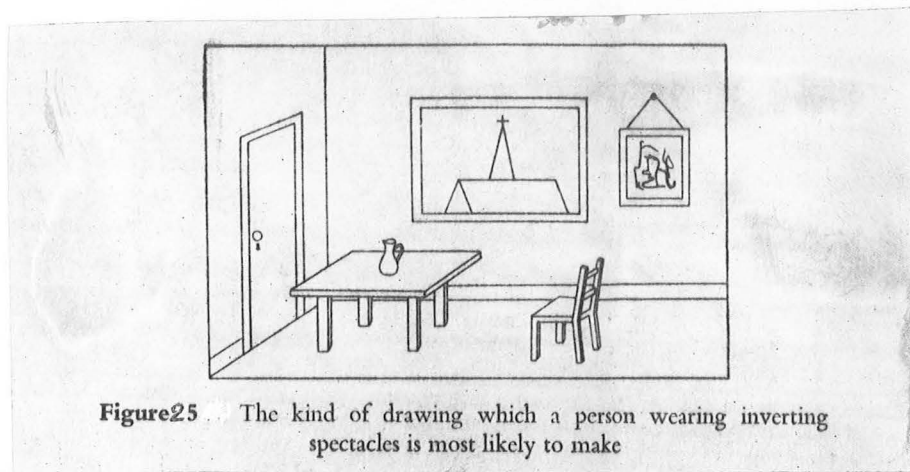
Walls (1951c) has argued, falsely I think, that complete adaptation to inversion is not possible because the structural features of the visual system are innate and immutable. He conceded (p.191 footnote) that behaviour associated with mono-oriented objects is entirely learned, so that he must have been thinking of something other than visual polarity when he concluded that full behavioural adaptation is impossible.

One of the reasons why Walls concluded that full adaptation is not possible may have been that he was looking for the wrong thing. He expected that full adaptation would imply in some way a geometrical shifting of the retinal image, what he called a "re-structuring of the visual field". It is not clear what Walls meant, but perhaps

he was referring to what Taylor insists happens to persons wearing inverting spectacles. Taylor (1962) maintains that when inverting spectacles have been worn for some time, objects which have been handled are reported to be erect, but objects which have not been handled are reported to be inverted. For instance, a person may be in a room and report that the contents of the room look erect, but that the scene outside the window looks inverted. Taylor maintains that this report implies that the subject will draw what he sees by drawing such a figure as figure 24. If this is what Walls refused to believe, I sympathize with his views, for Taylor is surely wrong. It is an error which many people make when thinking about these problems. Taylor is wrong because he confuses geometry with what we have called behavioural polarity. The subject whom Taylor described could not reveal the nature of his polarity responses in a drawing. The distinction between the inside and outside of the room is that only for objects inside the room has the subject's polarity behaviour become adapted. In terms of my operational tests, he will recognize objects in the room quickly, identify their tops and bottoms, predict their direction of fall, etc. The geometry of their position on his retina is unchanged, he has simply learned new polarity habits. Objects outside the window, having been seen less and handled less, elicit the old polarity habits. The subject cannot depict his change of polarity behaviour in a drawing, for no geometrical change is involved. His drawing of the room and the view outside will retain the same relative orientation of all its parts (see figure 25).



**Figure 24** The kind of drawing which a person wearing inverting spectacles may make according to Taylor and Papert



**Figure25** . The kind of drawing which a person wearing inverting spectacles is most likely to make

This same fallacy of regarding a change of polarity behaviour as a geometrical change equivalent to a geometrical righting of the image on the retina is the same fallacy which led Taylor and Papert to make false predictions about the consequences of head movements in inverted vision.

Taylor and Papert had no justification for their error, for all the published protocols of subjects wearing inverting spectacles stress that the 'polarity righting' of the field of view is not to be thought of as a geometrical shift of the visual field. One of Köhler's subjects (Kottenhoff, 1961) reported that things sometimes looked upright but that this did not mean that things appeared to turn round.

He said, "I see always the same but the interpretation is different". For this subject, distant objects had an unusual or upside-down appearance, while nearby, familiar objects had a right-way-up look about them. Köhler himself (1953), when describing the left-right appearance of things when wearing reversing spectacles wrote, "...but this isn't a sudden reversal; it remains the same picture experienced differently". For this subject, inscriptions on buildings or advertisements were still seen in mirror writing, but the objects containing them were seen the right way round. Vehicles seen as driving on the right (in Austria, this is correct) nevertheless carried licence numbers in mirror writing. Köhler commented that this is optically impossible and his attempt to give a pictorial reconstruction of the subject's report is very misleading, as he realised when he wrote "the purely pictorial impression remains reversed" (Köhler, 1955). These effects are not at all geometrically paradoxical; it is simply



a question of different left-right polarity habits holding simultaneously for different parts of the field of view. In the film which Erisman and Köhler produced, an experience is described (in a very misleading way) of a subject wearing inverting spectacles who was confronted with two faces, one erect, and the other inverted. At first the inverted face was reported to be erect and the erect one inverted; but when the owner of the erect face began to smoke a cigarette, the direction of the smoke was incompatible with the inverted appearance of the face, and it was suddenly reported to be erect and yet retain some inverted features. The hair had the appearance of a beard. At one point both faces were reported to be erect. Taylor (1962, p. 206) misinterprets this report by concluding that, "The erect face appeared to have acquired a beard, as if the crown of the head had failed to jump with the rest and now occupied the same space as the chin". Taylor admits in conversation that he thinks of this situation as one in which there is a reported change in the geometrical position of one part of the face in relation to other parts. I am convinced that his interpretation is wrong.

It should not be thought that these paradoxical effects cannot be experienced unless one is prepared to wear inverting spectacles for long periods. It is possible, by simply looking through one's legs backwards to gain some insight into what these reports mean. From this position, another person who is standing erect is reported as being upright in the 'intermodal upright' sense and also in the 'motor co-ordination' sense, but many people say that his face has the same upside-down polarity which an inverted face has. ~~In the~~

In the first two senses the face 'looks' upright, and yet it has an upside-down look about it. Some people are able to adopt either of two attitudes towards the polarity of a face seen between their legs, and this change of attitude may be brought about by a change in the orientation of the background. In the situation where two people look at each other through their legs, some people describe the other person as having upside-down polarity and others <sup>describe</sup> ~~see~~ him as having erect polarity. There is no question that any of these changes in behavioural polarity are accompanied by any geometrical changes in what is reported.

If one stands erect and looks at an upside-down face, one may report that the hair has a "beardy" look about it, and that the eye lids have a "mouthy" look. The face, though familiar, may not be recognizable and certainly facial expressions will be very difficult to judge. If the upside-down face is seen in its proper relative orientation in an upside-down picture in which there is plenty of background, an observer may describe it as having upright polarity; and at the same time, describe an erect face, outside the picture seen against the erect room, as also having upright polarity. Here are two faces, one  $180^{\circ}$  disoriented with respect to the other, and yet both eliciting the description of erect polarity. These are just the responses which one of K hler's subjects made. According to Taylor (private conversation) this type of behaviour implies that the subject will, when asked to draw what he sees, draw two faces in the same geometrical orientation.

In spite of my disagreement with Taylor, I have to admit that genuine geometrical shifts are sometimes reported. One of K hler's

subjects reported that after wearing left-right reversing spectacles a sort of mirror-writing appeared between lines of print. Another subject reported two points of light when only one was present, one in the position of the light and a dimmer one in the symmetrical position on the other side, and these were seen even monocularly. Taylor (1962) reported that Papert, while wearing reversing spectacles, saw two chairs, one on one side and one on the other. It seems more likely, when one looks at the details of what Papert reported, that the 'two chairs' were not both seen, but rather that one was felt and the other seen. It is difficult to see how the cases of diplopia reported by Köhler can be explained this way. Rapid eye movements may have been taking place, or the dim second light may have been an after-image or eidetic image. The problems raised by these reports must be considered in relation to the problem of monocular diplopia.

Walls had to admit that monocular diplopia is a very difficult fact to accommodate. I also admit the difficulty, but insist that even if monocular diplopia does exist as a consequence of distorted vision, this would have no connection with the problem of visual polarity. Such diplopia would be the result of the changed 'space values' of retinal points in relation to motor movements and other sense modalities. A change of polarity does not involve a change in the geometrical space values of the retina. We predict that monocular diplopia, if it occurs at all, will result when inverting spectacles are worn in a purely polyoriented, unpolarized visual environment.

Thus the question, 'do things appear upside-down' is a very

ambiguous one; the answer a subject gives will depend on his criteria of inversion. However, no one would describe a polyoriented, or unpolarized field of view as either upright or upside-down. It is unlikely that anyone would use these terms in such surroundings even if they knew that motor behaviour and intersensory judgments were disturbed. Polarity seems to be a necessary basis for the application of any ordinary verbal judgments of inversion.

Köhler contends that "Only through manipulation of objects does the simultaneously seen world obtain its directions; ..... he who wants to see correctly must first be able to manipulate correctly." (Köhler 1953, trans. by Gleitman, p. 19). Taylor's theory is also based on the necessity for movements and so also is Held's theory. The experiments necessary to prove this point of view have not been done. The following are outlines of some possible crucial experiments.

The polarity of the optical array may be inverted by simply placing a person in objectively inverted surroundings. Köhler had an inverted room made, but he does not seem to have used it for testing whether a change in behavioural polarity is dependent on manipulations. To be fully convincing, objects in an inverted room would have to fall upwards and smoke would have to descend.

The question is whether visual inspection alone would lead to new polarity habits, such as rapid and accurate recognition of objects, reading, the anticipation of the direction of falling objects, and a change in the choice of ambiguous figures, etc. If such changes occurred they would demonstrate that a change in polarity behaviour does not necessarily involve any manipulative activity or re-afferent stimulation. The training, in other words, would be purely ex-afferent

and not re-afferent. We predict that learning would take place under these circumstances, and that new polarity habits would be built up. Of course eye movements would occur and, although these are not normally thought of as "manipulations", they do give rise to re-afferent stimulation. To control for this factor and at the same time use a less complex visual input, one could test whether the speed of reading inverted writing improves when the print is moved intermittently across the subject's field of view while he wears a device which stabilizes the retinal images against the effects of eye movements. We would be very surprised if reading did not improve under these circumstances and, if it did, one would have to abandon any narrowly based theories of so-called perceptual learning, in which muscular manipulations or re-afference are thought to be essential.

This is not to say that in a mono-oriented, apparently inverted field of view, motor-adaptation and changing intersensory judgments would not contribute to a change of behavioural polarity. It seems from most of the protocols that a change of behavioural polarity occurs after many motor and intermodal adjustment have been made, although one of Köhler's subjects (Marte) reported new polarity habits on the first day. On the other hand, Kottenhoff did not report a change of polarity after 40 days of inverted vision, even though his motor behaviour was well adjusted. However, Kottenhoff described to Taylor (1962, p. 180) the technique he employed when he was asked to report on the left-right polarity of visible surroundings while wearing left-right reversing spectacles. According to Taylor, "Kottenhoff defined the positions of the edges of his field of vision as being next to his forehead, his nose, his right temple, and his left temple. Since these parts were not in his field of view, they constituted a frame of reference that

remained invariant throughout the experiment." Assuming that this invariance refers to the relationship between the felt position of the frame and the felt direction of gravity, it is not clear why this frame should necessarily have remained invariant throughout the experiment for this subject. It did not remain invariant for all subjects: Stratton and other subjects reported feeling as though they were standing on their heads.

I may have given the impression that I regard behavioural polarity as a unitary thing, but this is not so; a change in one aspect of polarized behaviour, for instance recognition speed, may occur without any change in another, for instance rapid prediction of the direction of fall. It is because of these multiple possibilities, that it is of little use to ask the subjects whether things look upright. If one does this, one will inevitably get ambiguous answers. The conflicting reports made by Köhler's subjects, and much of the dispute in the literature are probably due to the use of a concept of polarity which is not operationally defined.

My analysis so far has consisted in classifying the various habits which are affected by distortions of the optical array, and considering to what extent they become adapted to the distortion. It may seem that I have assumed that if all these habits became adapted to distorted vision, so that they functioned rapidly and accurately, the adult subject would in all senses be said to 'see the world the right way'. But this does not follow, because an adult subject will retain all the old habits which he has built up over the greater part of his lifetime. He can recall these habits

and when he does so, he will be able to report on the discrepancy between these old habits and the new ones. The old habits will remain the preferred standard of what is 'correct', because they have occupied the largest part of the subject's life. The new habits will, even when functioning as well as the old, be reported as upside-down, etc., when compared with the old. If the distorting devices were worn from birth or for many years, the adapted habits would be the only or the strongest standard of 'normality'. Such experiments have not been done, but it is difficult to see how they could do other than prove the correctness of *my* analysis.

A person who has had no other visual experience but through distorting devices, would, I suggest, be behaviourally indistinguishable from an ordinary person in almost all respects. His post-rotational nystagmus would probably be anomalous, and it is more than likely that he would be slower than the normal child in developing visual-motor skills, etc., and this would probably have a general retarding effect. Furthermore, it is probable that such a person would adapt to normal vision more quickly than a normal person adapts to distorted vision. These differences, if they were shown to exist, would demonstrate that the neonatal nervous system is structurally biased in favour of the normal visual-motor and intersensory relationships. In some respects, for instance vestibular-visual reflexes, this is known to be the case. There are good reasons for supposing that head and eye fixation reflexes are also built into the system. It is unlikely that the nervous system is a tabula rasa as far as spatial skills are concerned, and however successfully a human being could adapt to visual distortion, it would not prove that the nervous system is initially unbiased.

Disturbances of visual polarity may apparently occur as a result of cerebral injury. Klopp (1951) reviewed 13 papers from the clinical literature in which there were reports of patients who experienced their visible surroundings upside-down. Whether this affected their visual-motor co-ordination is not clear. The etiology and theoretical significance of this condition defy analysis at the present time.



## REFERENCES

- Allen, M. J. (1954). Dependence of cyclophoria on convergence, elevation and the system of axes. Amer. J. Optom. 31, 297-307.
- Ames, A. (Jr.). (1926). Cyclophoria. Amer. J. physiol. Opt. 7, 3-38.
- Ashby, W.R. (1957). An Introduction to Cybernetics. London: Chapman and Hall.
- Barnes, R. M. (1949). Motion and Time Study (3rd Ed.). New York: Wiley.
- Beller, H. K., and Morant, R. B. (1963). Adaptation to prismatically rotated visual fields. Typescript from Authors.
- Bishop, R. E. (1959). Immaturity and learning in the visual perception of direction. Ph.D. Diss., Univer. of Chicago.
- Bonin, G. V. (1950). Essay on the Cerebral Cortex. Springfield, Ill.: Thomas.
- Bosson, J., and Hamilton, C. R. (1963). Interocular transfer of prism-altered co-ordinations in split-brain monkeys. J. comp. physiol. Psychol., 56, 769-774.
- Brecher, G. A. (1934). Die optokinetische Auslösung von Augenrollung und rotatorischem Nystagmus. Pflüg Arch. Physiol., 234, 13-28.
- Carr, H. A. (1935). An Introduction to Space Perception. New York: Longmans-Green.
- Coyle, D. (1907). Upright vision and the inverted image. Psychol. Bull., 4, 97-99.
- Culbert, S. S. (1954). Directional after-effects following systematic distortion of the visual field. J. Psychol., 37, 81-93.
- Davies, T., and Marton, P. A. (1958). Recording compensatory rolling of the eyes. J. Physiol. 140, 27-28.
- De Kleyn, A., and Versteegh, C. (1924). A method of determining the compensatory position of the human eye. Acta otolaryng., Stockh. 6, 170-174.
- Ditchburn, R. W., and Fritchard, R. M. (1960). Binocular vision with two stabilized retinal images. Quart. J. exp. Psychol., 12, 26-32.
- Donders, F. C. (1870). Die Bewegungen des Auges, veranschaulicht durch das Phänophthalmotrop. v. Graefes Arch. Ophthal. 16, 154.
- Downer, J. L. de G. (1958). Role of corpus callosum in transfer of training in *Macaca mulatta*. Fed. Proc., 17, 37.

- Duke-Elder, S., and Wybar, K. G. (1961). System of Ophthalmology, Vol. II. Henry Kimpton, London.
- Ewart, P. H. (1930). A study of the effect of inverted retinal stimulation upon spatially coordinated behavior. Genet. Psychol. Monogr., 7, 177-363.
- Ewart, P. H. (1937). Factors in space localization during inverted vision. II. An explanation of interference and adaptation. Psychol. Rev., 44, 105-116.
- Fender, D. H. (1955). Torsional motions of the eyeball. Brit. J. Ophthal., 65, 65-72.
- Fischer, M. H. (1930). Messende Untersuchungen über die Gegenrollung der Augen und die Lokalisation der scheinbaren Verikalen bei seitlicher Neigung des Gesamtkörpers bis zu 360°. II. Mitteilung. Untersuchungen an Normalen. v. Graefes. Arch. Ophthal., 123, 476-503.
- Foley, J. P. (1940). An experimental investigation of the effect of prolonged inversion of the visual field in the rhesus monkey (*macaca mulatta*). J. genet. Psychol., 56, 21-51.
- Fox, B. H. (1951). Figural after-effects satiation and adaptation. J. exp. Psychol., 42, 317-326.
- Fraenkel, G. S., and Gunn, D. L. (1961). The Orientation of Animals. New York: Dover.
- Free, W. T., and Jones, G. M. (1959). A cine technique for measurement of eye movements in a dynamic environment. J. Physiol., 150, 2-3.
- Freedman, S. J., Rekosh, J. H., and Hall, S. B. (1965). Effects on hand-eye co-ordination of two different arm motions during adaptation to displaced vision. Percept. mot. skills.
- Fry, G. A., Treleaven, C. L., Walsh, R., Higgins, E. L., and Radde, C. A. (1947). Definition and Measurement of Torsion. (Special Report No. 2. Comm. on Nomenclature and Standards. Amer. Acad. of Optom.). Amer. J. Optom., 24, No. 7, Report No. 3, 24, No. 10.
- Giannitrapani, D. (1958). Changes in adaptation to prolonged perceptual distortion: a developmental study. Ph.D. Diss., Clark Univer.
- Gibson, J. J. (1933). Adaptation, after-effect and contrast in the perception of curved lines. J. exp. Psychol., 16, 1-31.
- Gibson, J. J. (1937a). Adaptation with negative after-effects. Psychol. Rev., 44, 222-244.
- Gibson, J. J. (1937b). Adaptation, after-effect, and contrast in the perception of tilted lines. II. Simultaneous contrast and the areal restriction of the after-effect. J. exp. Psychol., 20, 553-569.

- Gibson, J. J., and Radner, M. (1937). Adaptation, after-effects and contrast in the perception of tilted lines. I. Quantitative studies. J. exp. Psychol. 20, 453-467.
- Gibson, J. J., and Mowrer, O. H. (1938). Determinants of the perceived vertical and horizontal. Psychol., Rev., 45, 300-323.
- Gogel, W. C. (1956). The tendency to see objects as equidistant and its inverse relation to lateral separation. Psychol. Monogr., 70, (Whole No 411).
- Grahe, K. (1938). Raddrehung der Augen und Otolithenstellung beim Menschen. Acta otolaryng., Stockh. 26, 268-275.
- Graybiel, A., and Woellner, R. G. (1958). A new and objective method for measuring ocular torsion. Amer. J. Ophthalm. 47, 349.
- Greenberg, G. (1960). Visual induction of eye torsion, as measured by an after-image technique, in relation to visual perception of the vertical, Ph.D. Diss. Duke Univer.
- Hamilton, C. R. (1964). Intermanual transfer of adaptation to prisms. Amer. J. Psychol., 77, 457-462.
- Hamilton, C. R., and Bosson, J. (1964). Decay of prism after-effects. J. exp. Psychol., 67, 148-150.
- Harker, G. S. (1960). Two stereoscopic measures of cyclotorsion of the eyes. Amer. J. Optom. 49, 461-473.
- Harker, G. S. (1962). Apparent frontoparallel plane, stereoscopic correspondence, and induced cyclotorsion of the eyes. Percept. Mot. Skills, 14, 75-87.
- Harris, C. S. (1963a). Adaptation to displaced vision. A proprioceptive change. Ph.D. Diss. Harvard, (Abs.).
- Harris, C. S. (1963b). Adaptation to displaced vision: Visual, motor, or proprioceptive change? Science, 140, 812-813.
- Harris, C. S. (1964). Proprioceptive changes underlying adaptation to visual distortions. Amer. Psychologist., 19, 562(A).
- Heinemann, E. G., and Marill, T. (1954). Tilt adaptation and figural after-effects. J. exp. Psychol., 48, 468-472.
- Held, R. (1961). Exposure history as a factor in maintaining stability of perception and coordination. J. ner. ment. Dis., 132, 26-32.
- Held, R. (1963a). Correlated and de-correlated visual feedback in modifying eye-hand coordination. Paper to E.P.A.

- Held, R. (1963b). Movement-produced stimulation is important in prism-induced after-effects: a reply to Hochberg. Percept. mot. Skills, 16, 764.
- Held, R. (1963c). Localized normalization of tilted lines. Amer. J. Psychol., 76, 146-148.
- Held, R., and Freedman, S. J. (1963). Plasticity in human sensorimotor control. Science, 142, 455-462.
- Held, R., and Hein, A. (1958). Adaptation of disarranged hand-eye coordination contingent upon re-afferent stimulation. Percept. mot. Skills, 8, 87-90.
- Held, R., and Hein, A. (1963). Movement produced stimulation in the development of visually-guided behavior. J. comp. physiol. Psychol., 56, 872-876.
- Held, R., and Gottlieb, N. (1958). Technique for studying adaptation to disarranged hand-eye coordination. Percept. mot. Skills, 8, 83-86.
- Held, R., and Mikaelian, H. (1964). Motor-sensory feedback versus need in adaptation to rearrangement. Percept. mot. Skills, 18, 685-688.
- Held, R., and Rakosh, J. (1963). Motor-sensory feedback and the geometry of visual space. Science, 141, 722-723.
- Held, R., and Schlank, M. (1964). An attempt that failed to reproduce a study of disarranged eye-hand coordination. Percept. mot. Skills, 19, 301.
- Helmholtz, H. von. (1962). Treatise on Physiological Optics. New York: Dover.
- Hermans, T. G. (1943). Torsion in persons with no known eye defect. J. exp. Psychol. 32, 307-324.
- Hess, E. H. (1956). Space perception in the chick. Sci. American, 195, 71-80.
- Higginson, G. D. (1937). An examination of some phases of space perception. Psychol. Rev., 44, 77-96.
- Hochberg, J. (1963). On the importance of movement-produced stimulation in prism-induced after-effects. Percept. mot. Skills, 16, 544.
- Hofmann, F. B., and Bielschowsky, A. (1900). Über die der Willkür entzogenen Fusionsbewegungen der Augen. Arch. ges. Physiol. 80, 1-40.
- Hofmann, F. B., and Bielschowsky, A. (1909). Über die Einstellung der Scheinbaren Horizontalen und Vertikalen bei Betrachtung eines von schrägen Konturen erfüllten Gesichtsfeldes. Pflüg. Arch. ges. Physiol., 126, 453-473.
- Holst, E. V. (1954). Relations between the central nervous system and the peripheral organs. Brit. J. Anim. Behav., 2, 89-94.

- Holst, E. V., and Mittelstaedt, H. (1950). Das Reafferenzprinzip. Naturwiss. 37, 464-476.
- Howard, I. P. (1961). An investigation of a satiation process in the reversible perspective of revolving skeletal shapes. Quart. J. exp. Psychol., 13, 19-33.
- Hubel, D. H., and Wiesel, T. N. (1963). Receptive fields of cells in striate cortex of very young, visually inexperienced kittens. J. Neurophysiol., 26, 994-1002.
- Hyslop, J. H. (1897). Upright vision. Psychol. Rev., 4, 71-73 and 142-163.
- Javal. Cited in Nagel, 1896.
- Kleint, H. (1936). Versuche über die Wahrnehmung. Z. Psychol., 138, 1-34.
- Klopp, H. W. (1951). Über Umgekehrt und Verkehrtsehen. Dtsch. Z. Nervenheilk., 165, 231-260.
- Kohler, I. (1951). Über Aufbau und Wandlungen der Wahrnehmungswelt, insbesondere über "bedingte" Empfindungen. Wein: Rohrer.
- Kohler, I. (1953). Umgewohnung in Wahrnehmungsbereich. Die Pyramids, 5, 92-95, and 6, 109-113.
- Kohler, I. (1955). Experiments with prolonged optical distortions. Acta. Psychol., 11, 176-178.
- Kohler, I. (1956a). Orientierung durch den Gehörsinn. Die Pyramids, 5, 81-93.
- Kohler, I. (1956b). Die methode des Brillenversuches in der Wahrnehmungspsychologie; mit Bemerkungen zur Lehre der Adaptation. Z. exp. angew. Psychol., 3, 381-417.
- Kohler, I. (1962). Experiments with goggles. Sci. American, 206, 62-86.
- Kohler, W., and Emery, D. A. (1947). Figural after-effects in the third dimension of visual space. Amer. J. Psychol., 60, 159-201.
- Kohler, W., and Wallach, H. (1944). Figural after-effects: an investigation of visual processes. Proc. Amer. Phil. Soc., 88, 269-357.
- Kompanajets, S. (1928). Investigation on the counter-rolling of the eyes in optimum head positions. Acta. otolaryng., Stockh., 12, 332-350.
- Kottenhoff, H. (1957a). Situational and personal influences on space perception with experimental spectacles. I. Prolonged experiments with inverting glasses. Acta. Psychol., 13, 79-97.



- Kottenhoff, H. (1957b). Situational and personal influences on space perception with experimental spectacles. II. Semi-prolonged tests with inverting glasses. Acta. Psychol., 13, 151-161.
- Kottenhoff, H. (1961). Was ist richtiges Sehen mit Umkehrbrillen und in welchem Sinne stellt sich das Sehen um? Germany: Verlag Anton Hain, Meisenkeim am Glan.
- Krantz, F. (1930). Experimentell strukturpsychologische Untersuchungen über die Abhängigkeit der Wahrnehmungswelt vom Persönlichkeitstypus. Z. Psychol., 16, 105-214.
- Kunnappas, T. (1960). Scales for subjective distance. Scand. J. Psychol., 1, 187-92.
- Lit, A. (1959). The effect of fixation conditions on depth discrimination at scotopic and photopic illumination levels. J. exp. Psychol., 58, 476-81.
- Loring, M. W. (1915). An investigation of the law of eye-movements. Psychol. Rev., 22, 354-370.
- Ludvigh, E. (1953). Direction sense of the eye. Amer. J. Ophthal., 36, 139-143.
- McCord, F. (1953). The measurement of adjustive eye movements. Joint Proj. N. M. 001, 063.01, Report No. 31, Nav. Sch. Av. Med., Pensacol., Fla.
- McFarland, J. H. (1962). Visual and proprioceptive changes during visual exposure to a tilted line. Percept. mot. Skills, 15, 322.
- Merton, P. A. (1964). Absence of conscious position sense in the human eyes. Ch. 14 in Bender, M. B. (Ed.) The Oculomotor System. New York: Hoeber Medical Division.
- Merton, P. A. (1956). Compensatory rolling movements of the eye. J. Physiol. 132, 25-27.
- Mikaellian, H., and Held, R. (1964). Two types of adaptation to an optically-rotated visual field. Amer. J. Psychol., 77, 257-263.
- Miller, E. F. (1962). Counterrolling of the human eye produced by head tilt with respect to gravity. Acta otolaryng., Stockh., 59, 479-501.
- Morant, R. B., and Harris, J. R. (1965). Two different after-effects of exposure to visual tilts. Amer. J. Psychol., 78, 218-226.
- Morant, R. B., and Mikaellian, H. H. (1960). Inter-field tilt after-effects Percept. mot. Skills, 10, 95-98.
- Morant, R. B., and Mistovich, M. (1960). Tilt after-effects between the vertical and horizontal axes. Percept. mot. Skills, 10, 75-81.

- Mowrer, O. H. (1935). A device for studying eye-hand co-ordination without visual guidance. Amer. J. Psychol., 47, 493-495.
- Mulder, M. E. (1874). Over parallele Roibewegingen der Oogen. Acad. Proefschrift. Onderzoek. physiol. Laborat te Utrecht 3, 168 ff.
- Mulder, M. E. (1897). De la rotation compensatrice de l'oeil en cas d'inclination a droit ou a gauche de la tete. Arch. Ophthal., Paris, 17, 465-474.
- Myers, R. E., Sperry, R. W., and McCurdy, N. M. (1962). Neural mechanisms in visual guidance of limb movement. Arch. Neurol., 7, 195-202.
- Nagel, W. A. (1896). Über kompensatorische Raddrehungen der Augen. Z. Physiol. Sinnesorg. 12, 331-354.
- Noji, R. (1929). Ueber optisch erzwungene parallele Rollungen der Augen. v. Graefe's Arch. Ophthal., 122, 562-571.
- Ogle, K. N. (1946). The binocular depth contrast phenomenon. Amer. J. Psychol., 59, 111-26.
- Ogle, K. N. (1950). Researches in Binocular Vision. Philadelphia: Saunders.
- Ogle, K. N., and Weil, M. P. (1958). Stereoscopic vision and the duration of the stimulus. A.M.A. Arch. Ophthal., 59, 4-17.
- Paillard, J. (1960). The patterning of skilled movements. in Handbook of Physiology, vol. 3, 1679-1708. Amer. Physiol. Soc.
- Penfield, W. (1954). Mechanisms of voluntary movement. Brain, 77, 1-17.
- Peterson, J., and Peterson, J. K. (1938). Does practice with inverting lenses make vision normal. Psychol. Monogr., 50, (whole No. 225) 12-37.
- Polyak, S. (1955). Über das Verhalten der Hühner beim Tragen von Prismen. Ph.D. Thesis, Innsbruck.
- Pickford, R. W. (1956). Inverting vision. Bull. Brit. Psychol. Soc., No. 28, 68-71.
- Polyak, S. (1958). The vertebrate Visual System. Chicago: Univer. of Chicago Press.
- Prentice, W. C. H., and Beardslee, D. C. (1950). Visual 'normalization' near the vertical and horizontal. J. exp. Psychol., 40, 355-364.
- Quereau, J. (1954). Some aspects of torsion. A.M.A. Arch. Ophthal., 51, 783-788.
- Quereau, J. (1955). Rolling of the eye around its visual axis during normal ocular movements. A.M.A. Arch. Ophthal. 53, 807.

- Rekosh, J. H., and Held, R. (1963). Visual-spatial distortion produced by the sensory feedback accompanying locomotion. Paper read to the Eastern Psychol. Assoc.
- Rhule, W., and Smith, K.U. (1959b). Effects of inversion of the visual field on human motions. J. exp. Psychol., 57, 338-343.
- Rhule, W., and Smith, K.U. (1959a). Effect of visual pre-training in inverted reading on perceptual-motor performance in inverted visual fields. Percept. mot. Skills, 9, 327-331.
- Rock, I. (1956). The orientation of forms on the retina and in the environment. Amer. J. Psychol., 69, 513-528.
- Ruftes. Cited in Nagel, 1896.
- Silver, R. J., and Morant, R. B. (1962). Tactile and kinaesthetic tilt after-effects. Paper read to Eastern Psychol. Assoc. Atlantic City.
- Smith, K. U., and Greene, P. (1963). A critical period in maturation of performance with space-displaced vision. Percept. mot. Skills, 17, 627-639.
- Smith, K. U., and Smith, W. M. (1962). Perception and Motion. Philadelphia and London: Saunders.
- Snyder, F. W., and Pronko, N. H. (1952). Vision with Spatial Inversion. Wichita, Kansas: McCormick-Armstrong.
- Sperry, R. W. (1942). Reestablishment of visuo-motor coordinations by optic nerve regeneration. Anat. Rec., 84, 470 (A).
- Sperry, R. W. (1945). Restoration of vision after crossing of optic nerves and after contralateral transplantation of eye. J. Neurophysiol., 8, 15-28.
- Sperry, R. W. (1944). Optic nerve regeneration with return of vision in anurans. J. Neurophysiol., 7, 57-69.
- Sperry, R. W. (1948). Orderly patterning of synaptic associations in regeneration of intracranial fiber tracts mediating visuomotor coordination. Anat. Rec., 102, 63-76.
- Stone, L. S. (1944). Functional polarization in retinal development and its re-establishment in regenerating retinas of rotated grafted eyes. Proc. Soc. exp. Biol. Med. 57, 13-14.
- Stratton, G. M. (1907). Eye movement and visual direction. Psychol. Bull., 4, 155-158.
- Stratton, G. M. (1896). Some preliminary experiments in vision without inversion of the retinal image. Psychol. Rev., 3, 611-617.
- Stratton, G. M. (1897-). Upright vision and the retinal image. Psychol. Rev., 4, 182-187.



- Stratton, G. M. (1897b). Vision without inversion of the retinal image. Psychol. Rev., 4, 341-360 and 363-481.
- Taylor, J. G. (1962). The Behavioural Basis of Perception. New Haven and London: Yale Univer. Press.
- Taylor, J. G., and Papert, S. (1955). A theory of perceptual constancy. Brit. J. Psychol., 47, 216-224.
- Tourtual, J. (1840). Bericht über die Leistungen im Gebiete der Physiologie der Sinne, insbesondere des Gesichtssinnes. Muller's Arch. Anat. N. Physiol., 56.
- Vernon, M. D. (1934). The perception of inclined lines. Brit. J. Psychol., 25, 186-196.
- Wallach, H., Kravitz, J. H., and Lindauer, J. (1963). A passive condition for rapid adaptation to displaced visual direction. Amer. J. Psychol., 76, 568-578.
- Walls, G. L., (1951a). The problem of visual direction. I. The History to 1900. Amer. J. Optom., 28, 55-83.
- Walls, G. L. (1951b). The problem of visual direction. III. Experimental attacks and their results. Amer. J. Optom., 28, 173-212.
- Walton, W. G. (1948). Compensatory cyclo-torsion accompanying head tilt. Amer. J. Optom., 25, 525-534.
- Weinstein, S., Sersen, E. A., Fisher, L., and Weisinger, M. (1964). Is reafference necessary for visual adaptation? Percept. mot. Skills, 18, 641-648.
- Weinstein, S., Sersen, E. A., Weinstein, D. S. (1964). An attempt to replicate a study of disarranged eye-hand coordination. Percept. mot. Skills, 18, 629-632.
- Weinstein, S., Sersen, E. A., Weisinger, M., Fisher, L., and Richlin, M. (1964). Total adaptation to prismatic displacement in the absence of reafference. Typescript.
- Werner, H. (1938). Binocular depth contrast and the conditions of the binocular field. Amer. J. Psychol., 51, 489-97.
- Werner, H., and Wapner, S. (1952). Experiments on sensory-tonic field theory of perception. IV. Effects of initial position of a rod on apparent verticality. J. exp. Psychol., 43, 68-74.
- Wertheimer, M., and Arena, A. J. (1959). Effect of exposure time on adaptation to disarranged hand-eye coordination. Percept. mot. Skills, 9, 159-164.

- Wertheimer, M. (1912). Experimentelle Studien über das Sehen von Bewegung. Z. Psychol. Physiol. Sinnesorg., 61, 161-265.
- Wiesel, T. N., and Hubel, D. H. (1963a). Single-cell responses in striate cortex of kittens deprived of vision in one eye. J. Neurophysiol., 26, 1003-1017.
- Wiesel, T. N., and Hubel, D. H. (1963b). Effects of visual deprivation on morphology and physiology of cells in the cat's lateral geniculate body. J. Neurophysiol., 26, 978-993.
- Witkin, H. A. (1949). Perception of body position and of the position of the visual field. Psychol. Monogr., 63, (Whole No. 302).
- Winnow, M. (1871). Beiträge zur Lehre von den Augenbewegungen. v. Graefes Arch. Ophthal. 17, 233.
- Woodworth, R. S. (1934) (2nd. ed.). Psychology. New York: Holt.
- Wooster, M. (1923). Certain factors in the development of a new spatial coordination. Psychol. Monogr., 32, (whole No. 146).
- Wundt, W. (1894). Lectures on Human and Animal Psychology. Eng. Trans., London, p.114.